

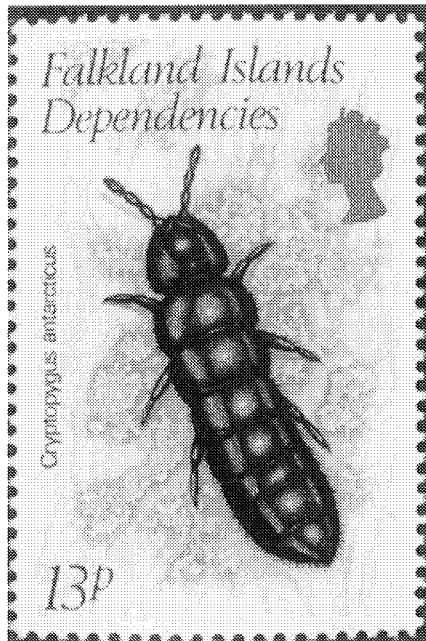
Biology of the Springtails (Insecta: Collembola)

STEPHEN P. HOPKIN

*School of Animal and Microbial Sciences
University of Reading*

Oxford New York Tokyo
OXFORD UNIVERSITY PRESS

1997



Cryptopygus antarcticus (Isotomidae), one of the most common terrestrial invertebrates in Antarctica. Reproduced by kind permission of the Falkland Islands Post Office and the Crown Agents Stamp Bureau.

Biology of the Springtails
(Insecta: Collembola)

*This book has been printed digitally and produced in a standard specification
in order to ensure its continuing availability*

OXFORD

UNIVERSITY PRESS

Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide in

Oxford New York

Auckland Bangkok Buenos Aires Cape Town Chennai
Dar es Salaam Delhi Hong Kong Istanbul Karachi Kolkata
Kuala Lumpur Madrid Melbourne Mexico City Mumbai Nairobi
São Paulo Shanghai Singapore Taipei Tokyo Toronto

with an associated company in Berlin

Oxford is a registered trade mark of Oxford University Press
in the UK and in certain other countries

Published in the United States
by Oxford University Press Inc., New York

© Stephen P. Hopkin, 1997

The moral rights of the author have been asserted

Database right Oxford University Press (maker)

Reprinted 2002

All rights reserved. No part of this publication may be reproduced,
stored in a retrieval system, or transmitted, in any form or by any means,
without the prior permission in writing of Oxford University Press,
or as expressly permitted by law, or under terms agreed with the appropriate
reprographics rights organization. Enquiries concerning reproduction
outside the scope of the above should be sent to the Rights Department,
Oxford University Press, at the address above

You must not circulate this book in any other binding or cover
and you must impose this same condition on any acquirer

ISBN 0-19-854084-1

Preface

I decided to write a book on Collembola early in 1992. At that time, I knew relatively little about springtails. However, it was clear from a sampling programme in which I was involved at the time that Collembola are present in huge numbers in soils and are of major ecological importance. Contrary to the assertion in the preface to *Biology of millipedes*, which I had recently completed with Helen Read (Hopkin and Read 1992), millipedes were not the only group of terrestrial invertebrates for which there has been no modern introductory text in English. The most recent general book on springtails was published by Paclt (1956) but this has long been out of print and is now out of date.

It is stated frequently in publications on springtails that the group are poorly studied in comparison to other arthropods. In fact I do not think that this is true since many aspects of their biology are quite well understood. Future work should focus much more on the gaps in our knowledge, especially the worldwide distribution of species, rather than on repeating earlier work. Hopefully this book will help to identify such gaps.

Those who study Collembola (whom I shall call collembologists) are fortunate in that all the publications on the group before 1962 were referred to by Salmon (1964). In his monograph, Salmon listed 2603 references. I had originally intended to try and emulate Salmon's achievement by compiling a complete list of post-1962 publications for this book. However, I discovered that there would have to be at least 5000 entries. Inclusion of them all would have greatly increased the length of the book so I decided to be selective. There are relatively few references to pre-1960 work as this can all be found in Salmon (1964). About 50% of publications from 1960 to 1979 are included; most of those I have left out are referred to in more recent papers on the same topic. About 90% of publications on Collembola between 1980 to 1989 are included (omitted are some single-species descriptions, a few local ecological surveys, and Russian language papers which I have been unable to consult directly). I have, however, referenced everything published since 1990 of which I am aware. Overall the reference list contains about 2500 entries.

Invertebrate biology is going through an extremely exciting period. The position of Collembola within the arthropods is the subject of much debate. The constraints of the Linnaean system of taxonomy are increasingly being questioned and the rapidly developing field of molecular biology is enabling scientists to examine the genes which control development, rather than just the products of their expression. Most research on the ecology of Collembola suggests that springtails are beneficial in promoting decomposition and soil fertility. Only a few species are pests. There is intense interest in the effects of chemicals on Collembola which are invariably non-target species. Indeed, a standard test for new chemicals using a

parthenogenetic strain of *Folsomia candida* has been developed and this is likely to be a legal requirement for certification of new chemicals in the not-too-distant future.

I hope that this book will be useful for applied ecologists who study Collembola in their work, and to invertebrate zoologists who are interested in springtails for the most important reason of all, curiosity.

Reading
April 1996

S.P. H.

Acknowledgements

I am sincerely grateful to all of the collembologists who responded to my reprint requests, especially those who sent complete collections of their work. In addition to sending numerous reprints, Peter Bellinger, Ken Christiansen, Louis Deharveng, Arne Fjellberg and Penny Greenslade kindly commented on sections of the book. I am particularly grateful to Penny for critically reading the first three chapters in such a helpful way. Thanks are also due to Peter Holland who read and commented on Section 3.2. However, any errors or opinions expressed are entirely my responsibility. Special thanks go to Peter Bellinger and Ken Christiansen who have maintained an up-to-date list of Collembola species for many years, and who kindly allowed me to use this when compiling the list of World genera in Appendix A.

Harold Gough (who by a happy coincidence lives in Reading) lent me his entire reprint collection comprising many hundreds of papers. This unselfish act saved me at least six months of library work. The only time when I had serious doubts about completing this project was when I arrived at Harold's house to discover that his collection was contained in 20 huge box files (I had envisaged something about a tenth of the size). They only just fitted into the boot of my car!

I would also like to thank the following people for sending copies of their papers: H.M. André, Javier Arbea, Anatoly Babenko, J.A. Barra, Thomas Bauer, Goran Bengtsson, Jean-Marie Betsch, Bill Block, Thomas Bolger, Gerhard Bretfeld, Paul Cassagnau, Erhard Christian, Romano Dallai, Wolfram Dunger, Gerhard Eisenbeis, Willem Ellis, Jack Faber, Juliane Filser, Geoff Frampton, Francesco Frati, Mari Manuela da Gama, Sigmund Hågvar, Veikko Huhta, Willy Humbert, Ryosaku Itoh, R. Jordana, Byung-Hoon Lee, John Lussenhop, Christian Kamplichler, J.A. Mari Mutt, Eduardo Mateos, Judith Najt, Pierre Nayrolles, Jose Palacios-Vargas, Henning Petersen, N. Poinso-Balaguer, J.F. Ponge, Leo Posthuma, M. Potapov, Sten Rundgren, Josef Rusek, Heikki Setälä, Peter Shaw, R.J. Snider, Felipe Soto, Yayuk Suhardjono, H. Takeda, J.-M. Thibaud, Nico Van Straalen, H. Uemiya, Guy Vannier, Herman Verhoef, Robert Waltz, Wanda Weiner, Paul Whalley, John Wiles, R. Yoshii, Jürg Zettel and D. Zinkler. Even single reprints were very useful and omission from the above list does not imply a lack of appreciation on my part. For those hard-to-get papers, the Interlibrary Loan staff at Reading University were very helpful.

I am also grateful to those collembologists who gave permission for figures and/or tables to be reproduced from their publications, especially Thomas Bauer, John Brackenbury, Gerhard Eisenbeis, Pierre Nayrolles, J.F. Ponge, H. Takeda and John Wiles who kindly loaned original diagrams, micrographs or negatives. The Photographic Unit at Reading University performed an excellent job in copying many of the figures.

David Knott gave me unhindered access to the Cole Library of Early Medicine and Zoology at Reading University (see Cole 1949) where I found several early references to Collembola. Paul Eggleton at the Natural History Museum, London, made available the excellent collection of reprints in the 'Aptera' section of the Entomology Department. Andrew Ross of the Palaeontology Department allowed me to examine specimens of the oldest fossil springtail *Rhyniella praecursor*, and to photograph Collembola preserved in amber in the impressive collection held by the Natural History Museum. Gina Douglas at the Linnean Society of London helped me to track down the earliest illustrations of Collembola by De Geer, and allowed me to copy illustrations from Linnaeus's personal copies of De Geer's works. I was also able to confirm that, unfortunately, there are no surviving specimens of 'Podura' in Linnaeus's collection of specimens in the strongroom at the Linnean Society. The Library staff at the Royal Entomological Society of London also helped in tracking down some nineteenth century references to Collembola.

Cathy Kennedy at Oxford University Press has supported me throughout the course of writing the book with only gentle reminders as the clock ticked towards (and past!) the contract deadline.

Finally, I would like to thank Peter Lawrence for his stimulating correspondence over recent years and his comments on the early chapters. Peter reminded me continuously of the importance of keeping an open mind. As he has so rightly said, 'cavities provide more space for bouncing ideas than do libraries'. For this and for other reasons, I dedicate this book to him.

Contents

1	General introduction	1
1.1	Overview	1
1.2	Key facts about Collembola	2
1.3	Ecological importance	5
1.4	Background reading	6
2	Review of the literature on springtails	8
2.1	Introduction	8
2.2	Publications before <i>Systema naturae</i> of Linnaeus (1758)	8
2.3	Linnaeus (1758) to Lubbock (1873)	12
2.4	Lubbock (1873) to Salmon (1964)	14
3	Evolution, systematics and biogeography	19
3.1	Introduction	19
3.2	Evolution of Collembola	19
3.3	Systematics of the Class Collembola	26
3.4	Families of Collembola	28
3.5	Biogeography	42
4	Ecomorphology and anatomy	46
4.1	Introduction	46
4.2	Morphology	47
4.3	Internal anatomy	58
4.4	Sense organs	64
4.5	Structure and function of the ‘spring’	70
5	Taxonomic methods and the species concept in Collembola	73
5.1	Introduction	73
5.2	Methods of defining species	74
5.3	Problems of defining species boundaries	85
5.4	The Subfamily Onychiurinae	93
5.5	Conclusions and recommendations	96
6	Interactions between Collembola and the abiotic environment	98
6.1	Introduction	98
6.2	Temperature	99
6.3	Water and salt balance	103
6.4	Gaseous exchange and metabolism	109

7	Interactions between Collembola and the biotic environment	113
7.1	Introduction	113
7.2	Feeding behaviour	113
7.3	Interactions between Collembola and other animals	123
7.4	The roles of Collembola in decomposition processes	127
7.5	Collembola as pests	129
8	Reproduction, development and life histories	133
8.1	Introduction	133
8.2	Reproductive organs, gametes and chromosomes	134
8.3	Mating behaviour and oviposition	136
8.4	Embryology	142
8.5	Postembryonic development and life histories	150
8.6	Ecomorphosis, epitoky and cyclomorphosis	153
8.7	Parthenogenesis and sex ratios	156
9	Ecology and conservation	158
9.1	Introduction	158
9.2	Observation and sampling techniques	158
9.3	Distribution of Collembola in space and time	160
9.4	Collembola as ecological indicators	173
9.5	Conservation	178
9.6	Cave Collembola	180
10	Ecotoxicology	183
10.1	Introduction	183
10.2	Laboratory toxicity tests with Collembola	183
10.3	Risk assessment	189
10.4	Effects of chemicals on Collembola in the field	192
10.5	Assimilation of chemicals by Collembola	196
10.6	Evolution of genetic resistance to chemicals	200
10.7	Conclusions	201
Appendix A	World genera of Collembola	202
Appendix B	Regional checklists of Collembola	221
Appendix C	Laboratory and field studies on the effects of chemicals on Collembola	226
References		232
Subject index		323
Systematic index		326

General introduction

1.1 Overview

Collembola are among the most widespread and abundant terrestrial arthropods. In this book, I shall cover all aspects of their biology and classification and show that their importance in terrestrial ecosystems has generally been underestimated. In this chapter, the main characteristics of the group are outlined and key publications are listed in which more detailed recent information can be found. Chapter 2 reviews the early literature on springtails from the first mention by Aristotle in about 350 BC via Linnaeus (1758) to the monograph of Salmon (1964).

The evolution of Collembola and theories as to their position within the Arthropoda are covered in Chapter 3. Chapter 4 describes their structure and function with special reference to the springing organ or furca, their most obvious feature. The taxonomy of Collembola is the subject of much debate. In Chapter 5, the problems of defining species and genera are discussed with an in-depth example of the Subfamily Onychiurinae where the greatest disagreements exist.

Chapters 6 and 7 examine interactions of springtails with the abiotic and biotic environments respectively. Collembola are remarkable in being able to survive at very low temperatures (some are cryptobiotic and survive immersion in liquid nitrogen) and this has enabled them to colonise extreme environments in the Antarctic continent. Most species feed on fungal hyphae or plant detritus and a few can be pests of economic importance.

Reproduction and development are reviewed in Chapter 8. Also covered are the phenomena of ecomorphosis, epitoky and cyclomorphosis when adult springtails alter their morphology and physiology in response to seasonal changes, reproductive activity and other factors. In recent years, Collembola have been put forward as sensitive indicators of environmental change and this proposal is examined critically in Chapter 9, together with a review of the literature on their local distribution, conservation and presence in caves.

With the exception of a few pest species, Collembola are considered to be useful organisms whose role in decomposition is beneficial to the long-term well being of soils. Several studies have examined the effects of chemicals on laboratory and field populations of Collembola. This rapidly expanding research area known as *ecotoxicology* is the subject of Chapter 10.

Three appendices are included. In Appendix A, a complete list of the Collembola genera of the world is given arranged in Families and Subfamilies. Recent taxonomic work is cited to allow workers interested in particular genera to locate the most recent descriptions of species and opinions as to their status.

Because of disagreement among taxonomists, a list such as this is unlikely to be completely uncontroversial. However, it will certainly assist initial passage through the complexities of Collembolan taxonomy. Appendix B cites recent checklists of springtails from specific countries and Appendix C includes publications concerned with the effects of chemicals on Collembola.

1.2 Key facts about Collembola

Collembola are currently considered to be a Class of the Phylum Arthropoda although their exact taxonomic position is still the subject of some debate. For the purposes of this book, after considerable thought and discussion with entomological colleagues, I have decided to follow a conservative line and to treat Collembola as insects (see Fig. 3.1). However, many of the old ideas on arthropod evolution are being reassessed in the light of modern evolutionary theory so the position of Collembola may change. For example, the theory that entognathy (mouthparts held within a buccal cavity of the head) is a synapomorphic character of Diplura-Protura-Collembola (Prabhoo 1987) is not supported by fossil evidence. This feature now seems to have evolved in parallel in Diplura and Protura-Collembola (Dallai 1994a).

The most obvious feature of Collembola is the jumping organ or furca (see Section 4.5). The furca evolved through the basal fusion of a pair of appendages on the fourth abdominal segment and is capable of propelling some springtails many times their own body length in a fraction of a second. The spring evolved as an escape mechanism to avoid predators. Species of Collembola confined to the soil have a reduced furca to ease their movement between soil particles and tightly packed leaf litter. Some have lost the jumping organ altogether.

All Collembola have a *ventral tube* which consists of eversible sacs derived from a pair of appendages on the first abdominal segment. This organ is extremely important in fluid balance (see Section 6.3) but can also function as a sticky appendage to enable springtails to adhere to slippery surfaces. In some species, the vesicles of the ventral tube may extend more than twice the length of the body and be used for self-righting after a jump (Brackenbury 1990). The scientific name for springtails was introduced by Lubbock (1873). He rightly considered the ventral tube to be the most characteristic feature of the group and gave them the name Collembola based on the Greek *colle* (= glue) and *embolon* (= piston).

Collembola are small animals. Most are only a few millimetres long although *Tetradontophora bielensis* (Onychiuridae) can reach 9 mm in length, and some members of the Subfamily Uchidanurinae grow to 10 mm and bear brightly coloured 'spines' (Greenslade 1991b). Indeed the opinion among some invertebrate zoologists that Collembola are rather dour unspectacular creatures is contradicted by the appearance of species such as *Morulina gilvipunctata* beautifully pigmented in cobalt blue or blue black (Yosii 1958), *Denisimeria longilobata* furnished with long lobes which project from the sides of the body, (Massoud 1964a), and the amazing *Paralobella ousseti* with transverse bands of yellow, red and white pigmentation (Cassagnau and Deharveng 1984). The tiniest and

least-pigmented species tend to be those that live permanently in the spaces between particles of soil or sand. Their small size gives them greater access to habitat space (Kamplichler and Hauser 1993).

The majority of springtails feed on fungal hyphae or decaying plant material. In the soil, they may influence the growth of mycorrhizae and control fungal diseases of some plants (see Section 7.2). In general, these effects are beneficial. However there are a few species, including *Sminthurus viridis* the 'Lucerne flea', which feed directly on plant material and can cause economic damage reducing yields of clover by up to 50% (Petersen 1971a; see Section 7.5). A number of species are carnivorous and eat nematodes, rotifers and even other Collembola (Cassagnau 1972a). A forensic scientist of my acquaintance says that springtails are abundant on human corpses during the early stages of decomposition (see also Folsom 1902).

There is one case in the literature of a patient who was diagnosed as harbouring an ectoparasitic population of Collembola in her hair after complaining of an itchy scalp for over a year (Greenberg 1985). However, the source of the 'infection' was discovered to be a plant pot at the head of the patient's bed which supported a healthy colony of an unidentified entomobryid springtail. The patient was 'cured' by spraying the pots with insecticide. Hurd (1954) accidentally infected his nasal sinuses with eggs of a species of *Isotoma* during fieldwork and passed about 50 live springtails from his nose some two months later. Pooterers beware!

Springtails are generally short-lived. Few survive as adults for more than a year or two. The documented longevity record is held by *Pseudosinella decipiens* which survived for up to 67 months in the laboratory (Barra 1976), although some cave species, or those in very cold climates, may live longer.

Approximately 6500 species of Collembola have been described although it is difficult to give an exact figure for three reasons. First there are many species yet to be discovered and described, especially in countries such as Australia and New Zealand where there is a high level of endemism (Greenslade 1991a; Salmon 1970a). Second, there is still some synonymy in particular families and there are likely to be species that have been described under more than one name. Third, there are differences of opinion among some taxonomists as to the degree of morphological difference between two specimens that represents separate species status. The latter two factors will tend to reduce the number of species. Overall, there must be many more undescribed 'good' species than synonyms or invalid species so the final figure is likely to be considerably in excess of 6500. The most recent estimate of the total number of species of all organisms on the earth quotes a figure of between 13 and 14 million, only 13% of which have been described (Heywood 1995). If the same ratio of described to undescribed species holds true for Collembola then there could be more than 50 000 species of springtail on our planet.

Several unusual species have been discovered in recent years. For example, *Gulgastrura reticulosa* from Korean caves (Lee and Kim 1995a; Lee and Thibaud 1987; Yosii 1966c), two species of *Isotogastrura* from sandy beaches in the West Indies (Thibaud and Najt 1992) and the Canary Islands (Fjellberg 1995b), and

Sturmius epiphytus from epiphytic moss in Columbian forests (Bretfeld 1994a) are so unlike previously described Collembola that new subfamilies have been erected to contain them (see Appendix A).

Collembola have a very wide global distribution. They are abundant on every continent, including Antarctica where *Biscoia sudpolaris* (Hypogastruridae) and *Antarctophorus subpolaris* (Isotomidae) have been found crawling among lichen at a latitude of 83° 55' S (Salmon 1962a), and more recently at 84° 47' S (Block 1984a), the most southerly location for any invertebrate. *Aackia karakoramensis* (Isotomidae) occurs on newly-fallen snow in the Himalayas at an altitude of 7742 m (Yosii 1966b). *Folsomides arnoldi* (Isotomidae) is abundant in Australian deserts (Suhardjono and Greenslade 1994).

Collembola are common on the sea shore. *Anurida maritima* (Fig. 3.6c) is a marine species and is one of the most familiar invertebrates of the littoral zone in Europe (Imms 1906). Leinaas and Ambrose (1992) caught 3200 specimens of *Archisotoma megalops* (Isotomidae) in a pitfall trap on a Spitzbergen beach in one hour at low tide. Several species live almost permanently on the surface of fresh water including the common and widespread *Podura aquatica* (Fig. 3.6d), a frequent sight on the surfaces of puddles after rain, sometimes in huge numbers likened to 'piles of soot' (McClachlan 1869; Shaw 1806). Species of *Hypogastrura* are abundant and clear growths from the percolation filters of sewage beds (Lawrence 1961a, 1970a). *Sinella curviseta* is common in waste water treatment trenches and may be an important contributor to the breakdown of organic matter (Nakamura 1984).

Many species live all their lives in the soil where they penetrate more than 150 cm below the surface (Gunn and Cherrett 1993; Snider *et al.* 1990). Others live on trees and are abundant in rain forest canopies (Guilbert *et al.* 1995). About one million Collembola of 16 species were collected by Palacios-Vargas and Gonzalez (1995) from 100 m² of dry forest in Mexico by insecticide fogging. Indeed while writing parts of this book in my garden in Reading, an average of three individuals per hour of *Entomobrya nivalis* (Entomobryidae) fell onto my laptop computer from the trees above.

Habitats with extreme climates such as deserts and polar regions support few species of Collembola but sites with many niches have a diverse springtail fauna. Collembola seem to follow the general rule that diversity is inversely related to latitude (Villalobos 1990) i.e. there are more species in tropical than in temperate zones. Deharveng *et al.* (1989) collected 135 species by soil extraction and hand-searching in a mountain forest in Thailand. In temperate forests diversity is lower but it is not unusual to find more than 40 species in deciduous woodland and mature grassland. For example 48 species of Collembola were found in Monks Wood National Nature Reserve in England (Lawrence 1973a), and 60 species in the Burren, Ireland (Lawrence 1961b). Gardens are usually rich in species. A brief collecting trip to Buckingham Palace gardens yielded 36 species (Lawrence 1963a) and the Royal Botanic Gardens at Kew, London probably has more species (70) than any other area of similar size in the British Isles (Lawrence *et al.* 1967).

The latter examples illustrate the dispersive powers of Collembola as most British and Irish species are relatively recent, post-glacial colonisers.

Collembola exhibit dominance patterns typical of most groups of terrestrial arthropods. The majority of individuals are usually represented by a small number of common species. In most populations, a large fraction of the species (usually >50%) are rare with dominance values of <1% (Hågvar 1994; Kopeszki and Meyer 1994; Takeda 1987; Fig. 9.8).

Collembola are most obvious when they 'swarm' (Brown 1921; Ellis 1976; Mari Mutt 1978a; Park 1949). Most reports are of species in the Family Hypogastruridae. They occur following synchronised reproduction in conditions of ideal humidity and temperature and abundant food supply (Baweja 1939). Maynard (1951) related a case in Switzerland where 'the wheels of a railroad locomotive were caused to spin on the rails due to the abundance of springtails'. A colour photograph of a large aggregation of *Hypogastrura meridionalis* is included in the paper of Dallai and Ferrari (1970).

There are numerous references in the literature to swarming, particularly on snow. Cuvier and Latreille (1838–1849) likened these aggregations to piles of gunpowder. Swarms certainly can be huge, often comprising several millions of individuals (Lyford 1975; Zettel and Zettel 1994a). Sankey (1952) observed a swarm of *Ceratophysella longispina* (Hypogastruridae) on a vertical chalk surface adjacent to a road in Surrey, England with a surface area of 35 m by 9 m at a density of 30–40 animals cm⁻² giving a total number of about 100 million individuals. The reasons for this behaviour are not completely understood although in most cases the Collembola are probably searching for a more favourable habitat. Hågvar (1995) suggested that *Hypogastrura socialis* migrates over snow and snow-covered ice (for the considerable distance of 200–300 m day⁻¹) as it allows the species to cross habitats which would otherwise represent physical barriers in the landscape (eg. rivers, wetlands and lakes).

1.3 Ecological importance

Collembola are extremely abundant in soil and leaf litter. In most terrestrial ecosystems they occur at densities of 10⁴–10⁵ m⁻² (Petersen and Luxton 1982). For example, in a meadow on heavy clay near Oxford, Ford (1935) found 60 000 m⁻². Densities of springtails of more than 10⁵ m⁻² have been found in pine forests in India (Reddy and Alfred 1989a) and Japan (Hijii 1994), moorland in England (Cragg 1961) and dry meadow in Norway (Fjellberg 1975a). In rainforest in Seram, Indonesia, Collembola comprised about 20% of the total number of arthropods on tree trunks, and 50% and 60% of the total from soil and leaf litter respectively (Stork 1988; Stork and Blackburn 1993). However, because of their small size the contribution of Collembola to total soil animal biomass and respiration is low, typically 1–5% in temperate ecosystems, but up to about 10% in some arctic sites and as much as 33% of total soil fauna respiration in ecosystems in early stages of succession (Petersen 1994). Typical values for the dry weight of

springtails in temperate ecosystems are 0.16 g m^{-2} in Danish beech woods (Petersen 1980) and 0.3 g m^{-2} in limestone grassland (Hale 1966a).

Despite their relatively low biomass, springtails are extremely important in influencing the structure of some soils (Rusek 1975a). For example, 'alpine pitch rendzinas' on limestone are composed mainly of a deep black humus layer of 15–20 cm in depth which is composed entirely of *Collembola* faeces (Kubiena 1953). Most soils contain millions of collembolan faecal pellets m^{-2} and these must be beneficial in slowly releasing essential nutrients to plant roots as the pellets are broken down by microbes.

The main effect of *Collembola* on decomposition and 'soil respiration' is through feeding on fungal hyphae (see Sections 7.2, 7.4). Lagerlöf and Andren (1991) calculated that in agricultural soils, *Collembola* consumed up to 1% of the annual microbial production (although they concluded that this was probably an underestimate). At certain densities of *Collembola*, grazing of mycorrhizae on roots can stimulate growth of the symbiont and improve plant growth (Lussenhop 1996). In other situations, *Collembola* may reduce disease by consuming pest fungi. For example, grazing by *Sinella curviseta* (Entomobryidae) on the cucumber fungus *Fusarium oxysporum* suppressed the infection and produced healthy plants in comparison to ungrazed controls which wilted badly (Nakamura *et al.* 1992).

Selective grazing by springtails may be an important factor limiting the distribution of certain species of basidiomycete fungi in the field (Newell 1984a). However, many of these effects are density-dependent and too little information is available for quantifying accurately the specific contribution of *Collembola* to 'indirect' or 'catalytic' decomposition (Petersen 1994). Nevertheless, the influence of springtails on decomposition and nutrient availability must be significant in many ecosystems.

1.4 Background reading

General textbooks on entomology understandably give relatively little space to *Collembola*. For example, Gillott (1995) and Gullan and Cranston (1994) devote about five pages each to springtails. One has to look elsewhere for more detailed accounts. The papers by Agrell (1963), Christiansen (1964a), Palissa (1964), Petersen (1965) and Schaller (1970) are useful sources of earlier references. Interesting discussions on various aspects of collembolan ecology, physiology and behaviour can be found in Cassagnau (1990a), Christiansen (1990, 1992a), Fjellberg (1985a), Greenslade (1991a), Joosse (1983), Joosse and Verhoef (1987), Petersen (1980, 1994), Poinso-Balaguer (1988), Rusek (1989a), Snider (1987), Verhoef (1995) and Waltz and McCafferty (1979).

The present book is designed to provide a general introduction to *Collembola* but it is not possible in the space available to treat all areas in great depth. This is particularly true of taxonomy and there are a number of works that should be consulted for further information. The most important of these is the monograph of Salmon (1964) which contains lists of all species, localities and publications on *Collembola* until about 1962. At the time of writing, this is still in print and avail-

able from the Royal Society of New Zealand at reasonable cost. Also essential are the series of papers by Stach (1947, 1949*a,b*, 1951, 1954, 1956, 1957, 1960*a*, 1963*a*) which deal with the springtail fauna of the world. These papers are widely available in libraries, often bound as a multi-volume set. The works of Ellis and Bellinger (1973, 1984) are indispensable. These give complete lists of all genera of Collembola described until about 1982 and give comprehensive information on synonymy.

Those with access to electronic mail should consider registering with the 'Collembola network' which is co-ordinated by Ken Christiansen and Peter Bellinger (e-mail address : christak@ac.grin.edu). A complete list of all the species of Collembola described to date, together with the biographical regions of the world where they have been found, can be downloaded from the network. I used this list to compile the table of world genera given in Appendix A.

A subscription to *Informations Apterygotologiques* is also useful (available from Laboratoire d'Ecologie Générale, MHNM, 4 avenue du Petit Château, 91800 Brunoy, France for a modest fee). Each issue contains a list of recent publications on Collembola (and other 'apterygotes') and is particularly important for tracking down papers in journals that are not indexed in computer databases.

Identification keys suitable for use by the novice are surprisingly few and far between. A good example is that by Fjellberg (1980*a*) but this deals with the Norwegian fauna only. Gisin's (1960*a*) key for European Collembola is very comprehensive but is difficult to use for identification of species in some families. In the Onychiuridae for example, Gisin gives specific status to a range of morphotypes with very subtle and difficult-to-discern differences. Christiansen and Bellinger's (1980) key to North American species is also useful for its copious illustrations.

Other particularly comprehensive keys or checklists have been published recently for Hawaii (Christiansen and Bellinger 1992), Italy (Dallai *et al.* 1995), Australia (Greenslade 1994*a*), the Iberian peninsula (Jordana *et al.* 1990), Poland (Pomorski and Skarzynski 1992) and the Neotropics (Mari Mutt and Bellinger 1990). For most countries, it is necessary to consult up-to-date papers on particular genera and these are given in Appendix A. A table of recent checklists, country by country, is given in Appendix B.

There are regular international meetings of collembologists at which the latest research is presented and discussed. A colloquium is held every four years. The Eighth International Colloquium on Apterygota was held in Helsinki in 1992 and was published in the volume edited by Vilkamaa (1994). Seminars on Apterygota are also held on a regular basis. The proceedings of three such meetings held in, Italy (Dallai 1986, 1989), and Poland (Sterzynska 1995) are particularly rich sources of quality papers on Collembola. However as a starting point, I would recommend the excellent *Atlas on the Biology of Soil Arthropods* by Eisenbeis and Wichard (1987). The section on Collembola contains numerous scanning electron micrographs of stunning quality, together with a wealth of interesting background information.

Review of the literature on springtails

2.1 Introduction

The earliest humans must have been aware of springtails. The 'Ice Man', whose well-preserved body was uncovered recently near the border between Austria and Italy, would have come across swarms of Collembola on alpine glaciers over which he roamed about 5000 years ago. However, rather like early stages in evolution which are lost forever if they leave no fossils, we will never know what early humans thought of these strange 'living carpets' of tiny animals since no written or artistic record survives.

The literature on springtails before Salmon (1964) can be divided into three main sections, each separated by works of major significance. The first (Section 2.2) comprises the pre-Linnean period before the publication of the tenth edition of *Systema naturae* in 1758. The second (Section 2.3) covers the period between 1758 and the monograph of Lubbock (1873) in which the term Collembola was introduced. After Lubbock, the rate of publication of work on springtails increased rapidly. By the end of the third period, Salmon (1964) was able to include 2603 references in his *Index to the Collembola*.

In the subsequent chapters of this book, I have concentrated on the 'post-Salmon' period. This is the era of the scanning and transmission electron microscopes which have transformed our understanding of the ultrastructure of springtails. I have included relatively few references to material published before the early 1960s. However, this is certainly not meant to imply that the work of these earlier scientists is unimportant. Indeed, when consulting Lubbock (1873) and Imms (1906), one is struck by the impression that but for the gentlemanly style of the language, one could be reading contemporary publications, such as their powers of observation and attention to detail.

2.2 Publications before *Systema naturae* of Linnaeus (1785)

The earliest written record of Collembola is probably that of Aristotle who lived from 384 to 322 BC. The English translation of *Historia animalium* by Smith and Ross (1910) includes a short passage that refers to swarms of 'snow fleas' which are 'reddish and hairy'. It is easy to understand how the theory of 'spontaneous generation' arose to explain the sudden appearance of huge numbers of springtails from barren ice and snow.

There are no other original observations on springtails published before the eighteenth century of which I am aware. I have scoured the works of Wotton

(1552), Moufet (1634), Aldrovandus (1638) and Topsel (1658) but to no avail. The translation of Jonstonus (1653) by John Rowland (Jonston 1657) includes a reference to spontaneous generation of 'red hairy worms on snow' but this is almost certainly copied from Aristotle. It is a great shame that neither Leeuwenhoek in his *Werken* (1684–1718) or Swammerdam in his *Bybel der nature* (1737–1738) brought their considerable observational powers to bear on Collembola. Hook (1665) illustrated a famous silverfish (Thysanura) in *Micrographia* but unfortunately no springtails leapt across his desk while he was examining specimens on his microscope, or if they did, he did not record the fact.

Many early descriptions are difficult to assign to the species we recognise today due to the ambiguity of the text and poor quality of the illustrations (if any). Collembola were often placed in the same category as fleas, aphids and other insects without wings. The first person to definitely describe Collembola was De Geer who in 1743 figured *Smynthurus fuscus* (*Allacma fusca*; Fig. 2.1). In a subsequent work (De Geer 1744), he named and illustrated four species (with probable modern equivalents in brackets), *Podura campestris nigra* (*Vertagopus arboreus*), *Podura campestris cinerea* (*Entomobrya nivalis*), *Podura aquatica nigra* (*Podura*

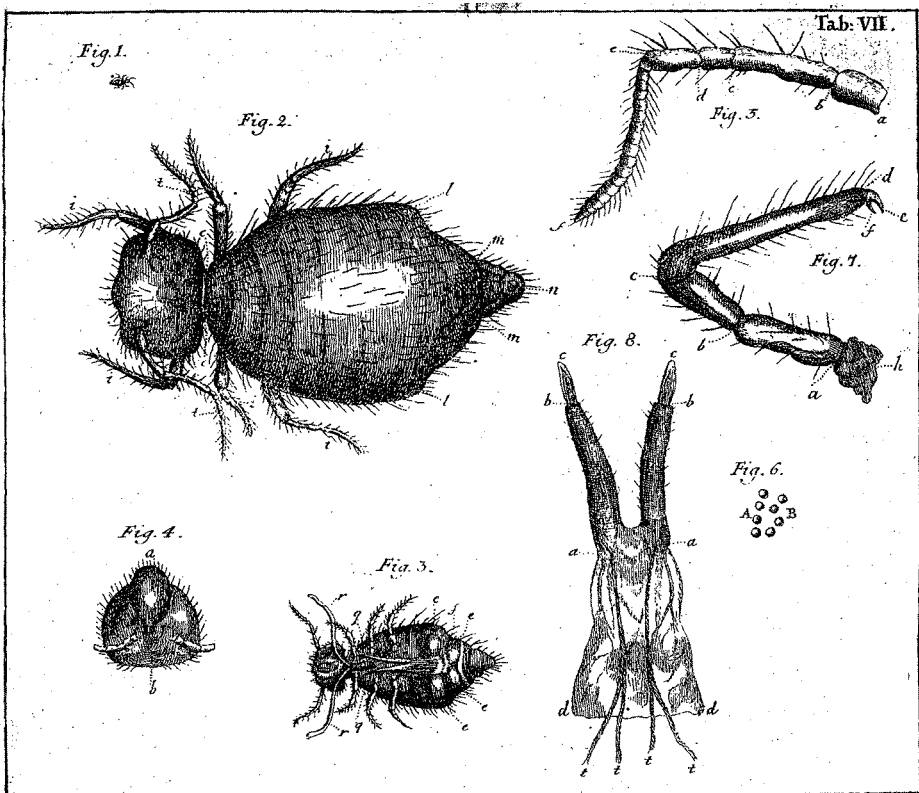


Fig. 2.1. '*Smynthurus fuscus*' (= *Allacma fusca*) (Sminthuridae) from De Geer (1743).

608

INSECTA APTERA. Lepisma.

VII. APTERA.

*Alæ nullæ, in omni sexu.*230. LEPISMA. *Pedes VI, cursorii.**Os Palpis II.**Cauda setosa: setis extensis.**Corpus squamis imbricatum.*sacchari- 1. *L. squamosa, cauda triplici.*na. *Brown. jum. 425. Setoura subargentea, cauda setosa, setis hirsutis.**Adam. microgr. t. 28. f. 147.**Habitat in America inter saccharum & utensilia domestica, inde per Europam vulgaris, hodie in Svecia inceptit.*terrestris. 2. *L. nuda, cauda triplici.**Habitat in Europa.**Similis Podura sed major, corpore toto albo cylindrico.**Antennæ corporis dimidii longitudine, obtusæ ut in Podura.*231. PODURA. *Pedes VI, cursorii.**Oculi II, compositi ex octonis.**Cauda bifurca, saltatrix, inflexa.*viridis. 1. *P. subglobosa viridis. Fn. suec. 1172.**Habitat in Europæ plantis.*atra. 2. *P. subglobosa atra, antennis longitudine corporis apice albis. Fn. suec. 1173.**Habitat in Europæ plantis.*fusca. 3. *P. globosa fusca nitida, antennis longis: articulis 3-urinis. Fn. suec. 1174.**Act. Stockh. 743. p. 296. t. 7.**Habitat in Europæ terrestribus.*

4. P.

Mutilla 220 quoniam aptera, hunc ordinem secundum adus intraret, sed character ordinis Hymenopterorum affinitas eam sociat.

Fig. 2.2. Pages 608 and 609 from the tenth edition of *Systema naturae* (Linnaeus 1758). Genus 231 *Podura* includes ten species now recognised as Collembola. For modern names of these species, see Systematic Index.

INSECTA APTERA. Podura.

609

- plumbea. 4. *P. teres fusco-carnlea nitida. Fn. succ. 1175.*
Habitat in Europæ arboribus.
- nivalis. 3. *P. oblonga cinerea signaturis nigris. Fn. succ. 1176.*
E. N. C. dec. 2. ann. 3. obj. 197. Pulex nivis.
De Geer Ad. Upf. 1740. p. 54. t. 2.
Habitat in Europæ nemoribus, Lignis.
- arborea. 6. *P. nigra, pedibus furcæque albis. Fn. succ. 1177.*
De Geer act. Upf. 1740 p. 49. t. 1.
act. Sæckb. 1740 p. 272. t. 1.
Habitat in Europæ sylvis.
- cincta. 7. *P. cylindrica grisea, cingulo atro antice albo.*
Habitat in sylvis Europæ.
- aquatica. 8. *P. nigra aquatica. Fn. succ. 1178.*
De Geer act. Upf. 1740 p. 57. t. 3.
Stæckb. 1740. p. 279. t. 3, 4.
Habitat in Aquas Europæ.
- finetaria 9. *P. terrestris alba. Fn. succ. 1180.*
Habitat in terra prægnante Europæ, frequens primo vere.
- ambu- 10. *P. alba, furca extensa. Fn. succ. 1170.*
 lans *Habitat in Europa.*

232. TERMES. *Pedes* VI, *curforii*.*Oculi* II.*Antenne* fetaceæ.*Os* maxillis duabus.

- fatale. 1. *T. luteum; alterius maxillis longitudine antennarum.*
Habitat in Indiæ utriusque umbrosis, aperto acri inveni-
sum, fornices cylindricos progrediendo inædificans, ma-
xillis longis altissime resiliens; Nidos e sabulo, sinu-
bus dædaleis in tophum struens. Destruit utensilia
omnia, utriusque Indiæ calamitas summa: domos, na-
ves, cibaria, vestimenta, ex animalibus & vegetabi-
libus singula quæque, relicta sola superficie integra;
calce viva coercendum, de quo Rolander & peregrina-
tores plurima.

Q q

Alic-

aquatica) and *Podura aquatica cinerea* (*Isotomurus palustris*). These illustrations were reproduced subsequently in Volume 7 of De Geer's *Memoires pour servir à l'histoire des insectes* published posthumously in 1778.

Hill (1752) described (but did not illustrate) 23 species of 'puceron' but only four of these merited more than a sentence. A few of Hill's species can be assigned to modern day equivalents but the descriptions of most are too brief to recognise. However, Hill's *Podura nigrescens antennis brevibus* 'The Water Puceron, the black *Podura* with short antennae' contains a cross reference to De Geer's *Podura aquatica nigra*, an early example of the use of scientific nomenclature to avoid misunderstanding. Hill also mentions that this species is 'common in ponds, and other standing waters; the surfaces of which are sometimes, in calm days in autumn, almost covered with the multitudes of it'.

2.3 Linnaeus (1758) to Lubbock (1873)

The Swedish naturalist Carl von Linné was born in 1707. He preferred the latinized version of his name and is known universally as Linnaeus, the founder of the binomial system of classification. In fact the first edition of his *Systema naturae* was published in 1735 when Linnaeus was only 28 years of age. However it is the tenth edition of *Systema naturae* published in 1758 which is regarded as the starting point for the modern system of taxonomy of multicellular animals (there are different dates for some other groups of organisms; see Quicke 1993). In the tenth edition, the *Regnum Animale* (Animal Kingdom) was divided into six classes. 1. Quadrupedia, 2. Aves, 3. Amphibia, 4. Pisces, 5. Insecta, and 6. Vermes. The Insecta were subdivided into seven orders namely Coleoptera, Hemiptera, Lepidoptera, Neuroptera, Hymenoptera, Diptera and Aptera. The Aptera contained all 'wingless insects' (including arachnids, woodlice, crabs and myriapods, as well as true insects such as termites, lice and fleas) and was divided into 14 genera (numbers 230 to 243 inclusive). *Generum 231, Podura*, contained ten species of what we now recognise as Collembola (Fig. 2.2).

It is interesting to note that the total number of species of animals in the world known to Linnaeus in 1758 was nearly 4400, considerably less than the 6500 or so species of Collembola that have been described to date (Appendix A). Further editions of *Systema naturae* were published in subsequent years. The fifteenth edition which appeared in three volumes was published between 1766 and 1770 and was the last produced under Linnaeus's supervision. He died in 1778.

Scientific study of animals and plants blossomed after the publication of *Systema naturae*. Monumental works were produced which attempted to describe and classify the natural world and all its living creatures. Collembola feature in some of these although it is often difficult to identify the modern day equivalents of the species as many are poorly described (e.g. Cuvier and Latreille 1838–1849; Geoffroy 1762, 1799; Gervais 1844; Müller 1776; Oken 1833–1842; Shaw 1806). Ledermüller's (1764) charming figure of a springtail (Fig. 2.3) is obviously *Podura aquatica*, but features such as the eyes and number of segments have, to put it mildly, been interpreted artistically! However, this is probably the earliest

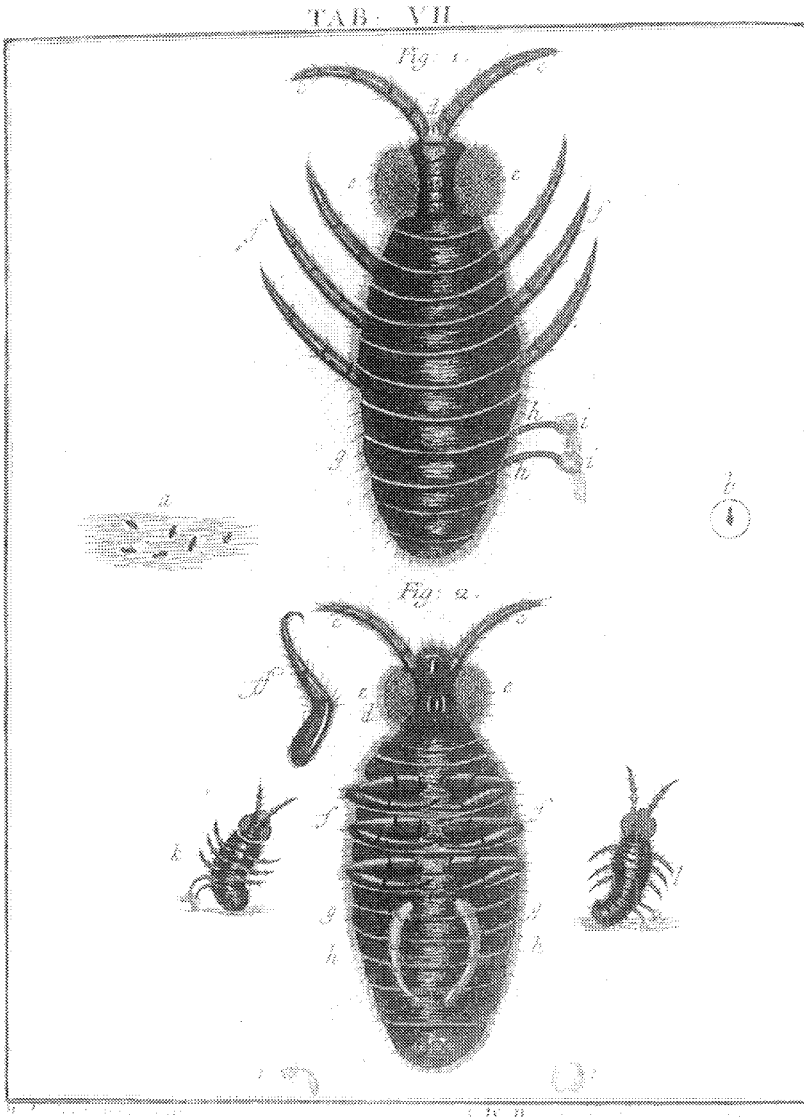


Fig. 2.3. *Podura aquatica* (Poduridae) from Ledermüller (1764).

colour illustration of a recognisable species. Schaeffer (1766) and Barbut (1781) each contain a small colour figure of '*Podura villosa*', the *Orchesella villosa* of modern terminology.

The ambiguity of many early descriptions, together with a lack of type specimens, has caused considerable taxonomic confusion. For example there are no Collembola in Linnaeus's surviving collections in Sweden or in the Linnean Society of London. In the days before telephones and a reliable mail service, a

worker in one country was often unaware that the species to which he or she had given names had already been described elsewhere. Lubbock (1873) drew particular attention to the synonymy that arose due to the simultaneous publications of Bourlet (1839, 1843) and Nicolet (1847). However, the great majority of cases of synonymy of genera have been resolved (Ellis and Bellinger 1973, 1984). Nicolet (1847) was notable for his attention to detail, in particular the beautiful Plate 6 which illustrates 12 species of Collembola in colour. Other early attempts at classifying springtails include those of Agassiz (1842–1846), Lamarck (1801), and Latreille (1806, 1810).

What was needed around the mid to late nineteenth century was a consolidation of ideas, a rationalisation of the taxonomy, and a single authoritative source which collembologists (as they were soon to become) could consult for basic information about the group. This was provided by Sir John Lubbock (Lord Avebury) in his *Monograph of the Collembola and Thysanura* published by the Ray Society of London in 1873.

2.4 Lubbock (1873) to Salmon (1964)

Sir John Lubbock was one of the most famous scientists of his time. He held several important posts including Vice Chancellor of the University of London and was President of the Royal Society. He had already published four *Notes on the Thysanura* (Lubbock 1862*a,b*, 1868, 1869) before the appearance of his *Monograph* in 1873. All collembologists should read this book. It contains the first use of the term Collembola, a wealth of original scientific observations, together with a series of beautiful black and white and colour plates (e.g. Figs. 2.4–2.6) painted by a ‘Mr. Hollick, a gentleman who is unfortunately deaf and dumb, but in whom these terrible disadvantages have been overcome by natural genius’ (Lubbock 1873). There are also black and white engravings by a ‘Mr. R. Beck’ of the scales of eight species, a popular subject for Victorian microscopists. Lubbock gives a critical account in his *Monograph* of earlier attempts to classify Collembola and includes some of the first drawings of internal anatomy.

Lubbock was a great friend of Charles Darwin. However, it is clear from the following passage on Collembola taken from page 348 of Volume I of the first edition of *The descent of Man* (1871) that Darwin did not share Lubbock’s affection and respect for springtails. ‘The members of this Order are lowly organized for their class. They are wingless, dull-coloured, minute insects with ugly, almost misshapen heads and bodies. Their sexes do not differ; but they offer one interesting fact, by shewing that the males pay sedulous court to the females even low down in the animal scale.’

Lubbock (1873) listed a total of 130 species for the world, but this number increased rapidly as collectors explored ever more remote parts of the globe. Collembola were discovered in North American caves (Packard 1888), and on the Antarctic continent by a British expedition in 1899 (Wise 1967). Lubbock himself published observations on Collembola from Spitzbergen (1898), and Tasmania and New Zealand (1899). Schött (1893*a*) reviewed the systematics and distribu-

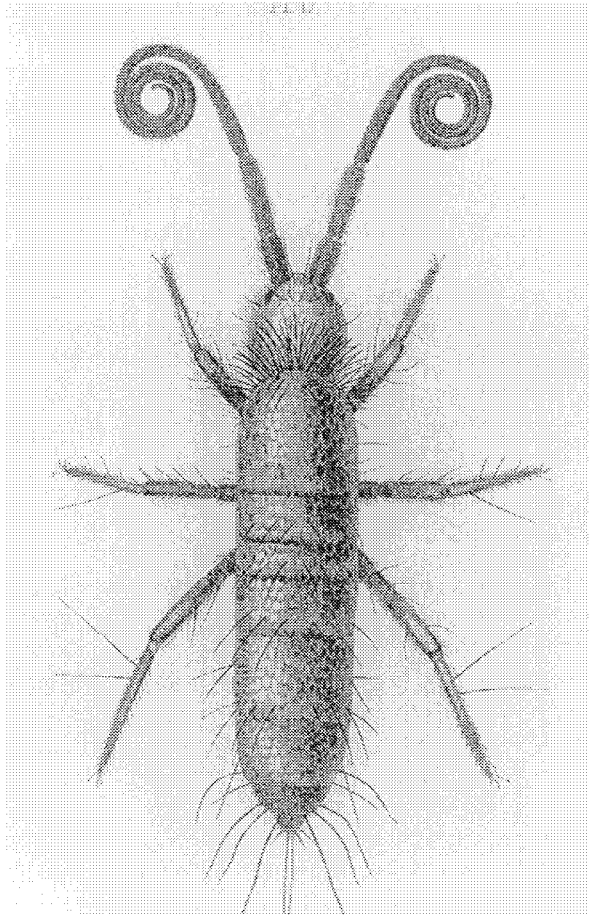


Fig. 2.4. *Pogonognathellus longicornis* (Tomoceridae) from Lubbock (1873) (cf. Fig. 3.12).

tion of Palearctic Collembola and described two new species from the 'Indischen Archipel' (Indonesia) (Schött 1893b). Checklists for individual countries and regions began to appear such as those for Finland (Axelson 1907; Reuter 1895), Scotland (Reuter and Reuter 1880), and Minnesota in the USA (Guthrie 1903). By the end of the nineteenth century, Carpenter and Evans (1899) estimated that 75 species of Collembola had been recorded in the British Isles alone.

Interest in taxonomy of springtails blossomed up to and including the period of the First World War. Many genera with which we are familiar today were described in this period such as *Anuridella* (Willem 1906), *Brachystomella* (Ågren 1903), *Friesea* (Dalla Torre 1895), *Mesachorutes* (Absolon 1900), *Odontella* (Schäffer 1897), *Protaphorura* (Absolon 1901) and *Tomocerura* (Wahlgren 1901). Börner was particularly active in describing numerous species and genera including *Mesaphorura* (1901a), *Willemia* (1901b), *Protanura* and *Lobella* (1906a). He

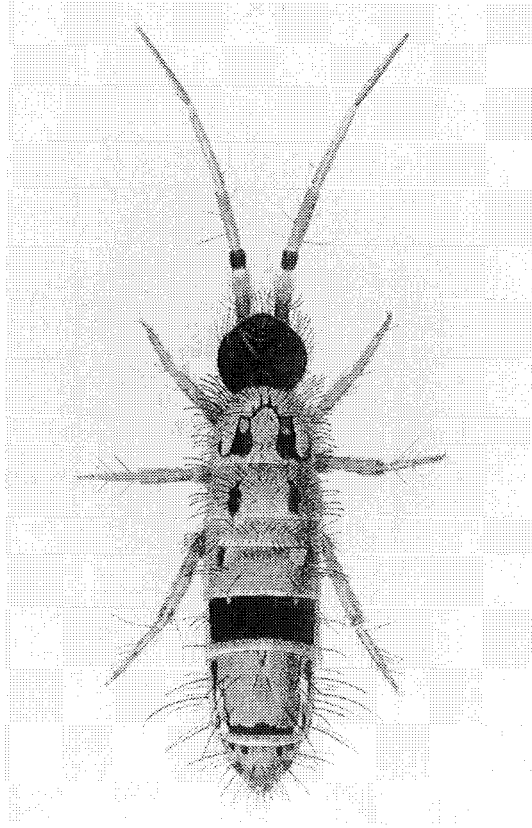


Fig. 2.5. *Orchesella cincta* (Entomobryidae) from Lubbock (1873).

also laid the foundation for modern classification by introducing the families Isotomidae, Cyphoderidae, Tomoceridae and others (Börner 1913). Several invertebrate zoologists studied the internal anatomy of Collembola and produced work of lasting scientific value. For example, the monograph on *Anurida maritima* by Imms (1906) contains descriptions of the embryological development and internal anatomy of this common marine springtail and is illustrated by seven detailed coloured plates. Collembola later featured prominently in his famous *Textbook of entomology* (Imms 1925).

It is not possible in the space available to give more than a brief flavour of the huge body of work produced between the end of the First World War and the publication of Salmon (1964). However, looking through Salmon's list, which included everything published on Collembola up until that time, it is clear that attention should be drawn to certain workers who made a major impact on the field.

J.T. Salmon himself described numerous species from many countries and wrote the first major review of the Collembola of New Zealand (Salmon 1941).

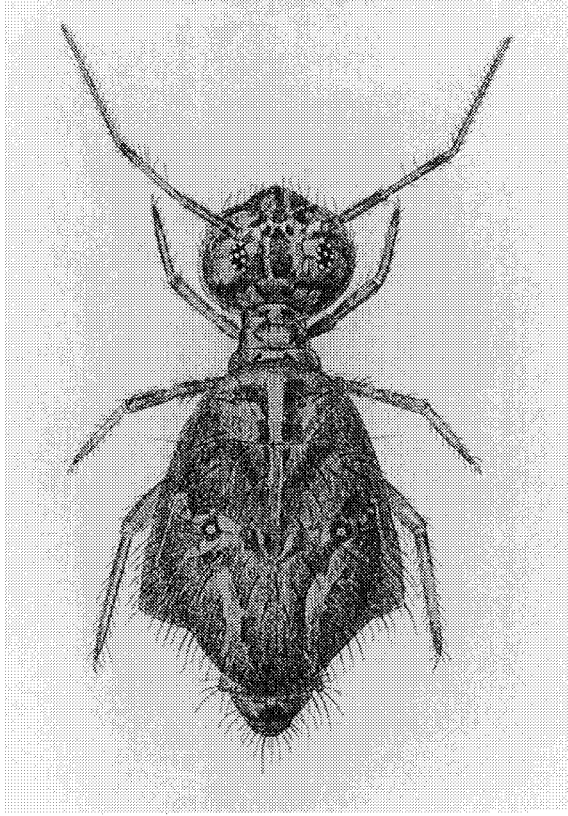


Fig. 2.6. *Sminthurus viridis* (Sminthuridae) the 'Lucerne flea' from Lubbock (1873).

G.H. Carpenter published some 40 papers between 1895 to 1943 on Collembola from all corners of the globe including Antarctica (Carpenter 1921). J.W. Folsom produced a similar number of publications over the same period and conducted a major revision of the Family Isotomidae (Folsom 1937). E. Handschin published extensively between 1919 and 1958 and wrote the volume on 'Apterygota' for the series *Die Tierwelt Deutschlands* (Handschin 1929). H. Womersley began his studies in Britain in 1923 but by 1943 had published 48 papers describing Collembola from many parts of the world including Australia, New Zealand and Africa.

Important monographs on the Collembola of Iowa and New York State were written by Mills (1934) and Maynard (1951) respectively. World Collembola were studied extensively by J.R. Denis (75 papers between 1921 and 1951) and C. Delamare Deboutteville who had 69 papers listed in Salmon (1964) and continued to publish work on Collembola into the late 1960s (Weiner 1992). J. Stach (who in 1904 published the first of many papers) reviewed the Collembola of the world in nine instalments between 1947 and 1963. Last but not least, H. Gisin wrote a

checklist of Holarctic Collembola (Gisin 1944), a comprehensive key to European species (Gisin 1960a) and a series of papers 'Collemboles d'Europe' for the journal *Revue Suisse de Zoologie* throughout the 1960s.

Collembola began to feature in studies on soil ecology during this period (e.g. Agrell 1941; Ford 1935; Glasgow 1939; Morris 1922, 1927; Thompson 1924). Some of the earliest applied ecological research was conducted in Australia on the 'Lucerne Flea' *Sminthurus viridis* (see Fig. 2.6). This species was introduced to Australia from Europe and caused major economic damage to crops (Davidson 1934; Davies 1928a; Holdaway 1927; MacLagan 1932; Womersley 1933, 1934).

The subsequent chapters of this book concentrate on work published from the mid 1960s to the present day. Nevertheless, it is important to recognise that without the foundations laid by the individuals cited above (and others too numerous to mention) modern research on Collembola would be impossible. There is a regrettable tendency nowadays to ignore older literature for being 'out of date'. However, I would strongly recommend that readers of this book search out some of the early literature for its scientific (and occasional entertainment!) value. Work such as Lubbock (1873) is evocative of a time when research was conducted at a more leisurely pace.

Evolution, systematics and biogeography

3.1 Introduction

There is currently a vigorous debate on the phylogeny of arthropods. Many old ideas are being overturned following molecular analysis of relationships between extant arthropod groups and discovery of new fossils. In recent years, there has been a welcome trend towards taking a much broader cladistic view of evolution, rather than forcing different arthropod groups into strict Linnaean categories (Queiroz and Gauthier 1994). In this chapter, the origins of Collembola and their relationship to other arthropods are discussed (Section 3.2). The systematics of Collembola themselves is examined (Section 3.3) and the main characteristics of each family are outlined (Section 3.4). Finally, an overview is given of the biogeography of Collembola together with a discussion of the problems involved in determining past and present day distributions of the different species (Section 3.5).

3.2 Evolution of Collembola

3.2.1 *The position of Collembola within the Arthropoda*

Collembola and other 'soft bodied' arthropods are rarely preserved as fossils. Reconstructions of phylogenies rely mostly on comparisons between living examples of the different classes of arthropods. Almost all taxonomists now agree that the most appropriate way to study these relationships is by *cladistics* (see Cranston *et al.* 1991; Disney 1983, 1994; Forey *et al.* 1992; Minelli 1993; Quicke 1993). It is universally accepted that the Class Collembola is a *monophyletic group* (i.e. derived from a single common ancestor – see Section 3.3). However, the position of springtails in relation to other arthropods is hotly debated and almost every possible scenario has been proposed at some time or other. The phylogeny proposed by Kristensen (1991), Kukalová-Peck (1987, 1991) and others is based on sound cladistic principles (Fig. 3.1), but previous experience would suggest that it is not cast in stone! Indeed the monophyletic status of Diplura has recently been questioned (Bilinski 1993; Stys and Bilinski 1990). What is certain is that the group 'Apterygota' comprising the extant Collembola, Protura, Diplura, Archaeognatha and Zygentoma (Thysanura) is not monophyletic and should be abandoned as a formal category.

The great majority of arthropod phylogenies have been developed from studies of comparative anatomy, both external and internal. One of the main problems associated with this approach is *homoplasy*, sometimes called 'convergent evolu-

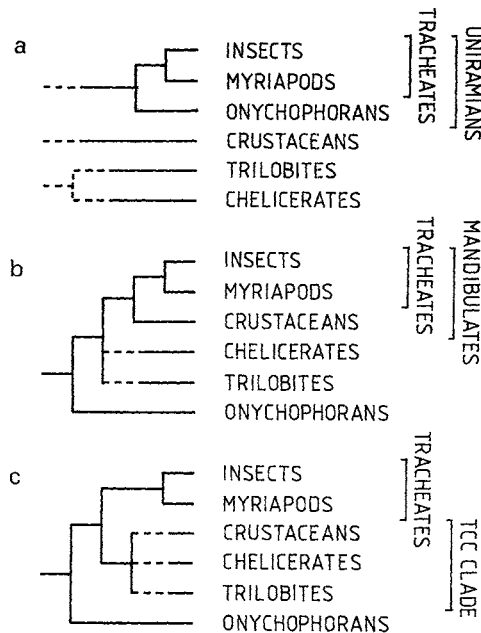


Fig. 3.2. Phylogenetic relationships of the main arthropod groups. The three main alternative hypotheses are represented: (a) the polyphyletic-uniramian tree, (b) the 'mandibulate' tree, and (c) the 'TCC' tree. The branch lengths are arbitrary. Redrawn from Averof and Akam (1995b) by kind permission of the authors and the Royal Society of London.

ferent from their close relatives), it is clear that one should not rely entirely on comparative anatomy when constructing phylogenies (Telford and Thomas 1995). Gene sequence data have been widely seen as a panacea for this problem. Changes in gene sequences are thought to be largely unaffected by the environment, with the result that similarity of DNA sequences may more accurately reflect relationships (Avice 1994; Margulis 1992; Telford and Thomas 1995). However it is important to remember that a given gene may be informative at one taxonomic level, but uninformative at another (Soto-Adames *et al.* 1994).

Three recent studies using molecular techniques have reinforced the view that the Arthropoda is a monophyletic group (Boore *et al.* 1995; Friedrich and Tautz 1995; Giribet *et al.* 1996). However scenarios of evolutionary pathways within arthropods have been put in the melting pot following the discovery by these and other authors of an apparently closer relationship between Crustacea and Insecta than has hitherto been assumed (e.g. Fig. 3.3). While one should caution against rejecting all previous schemes (only a relatively small number of species have been analysed to date), the molecular evidence for a 'crustacean-like' ancestor of Collembola and other 'hexapods' is compelling. This work certainly calls into question the hitherto assumed close relationship between Myriapoda and insects (e.g. Palacios-Vargas 1991a,b).

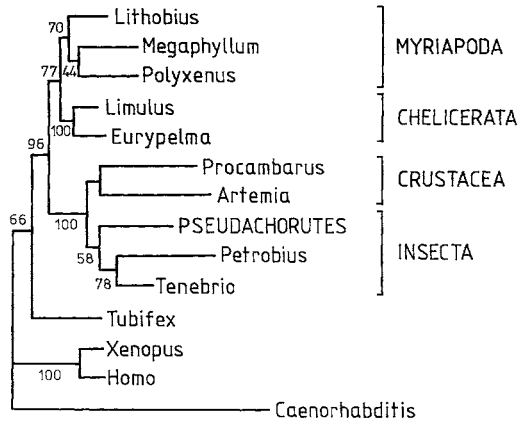


Fig. 3.3. Phylogenetic relationships of the arthropod taxa as estimated from 18S and 28S rDNA sequences (Collembola represented by *Pseudachorutes* sp.). Numbers at the branches correspond to the percentage bootstrap support from 100 replications with the maximum likelihood algorithm. Redrawn from Friedrich and Tautz (1995) by kind permission of the authors and Macmillan Magazines.

Some morphological features of Collembola support a close relationship with Crustacea. The composed eye of Collembola is a reduced compound eye which has been shown to be remarkably similar in structure to crustacean eyes (Paulus 1972). Young embryos of *Anurida maritima* have a small pair of appendages on the so called 'intercalary segment' which is probably homologous to the second antennal segment of Crustacea (Tamarelle 1984). These transient appendages may represent the second antennae of crustaceans which were 'lost' during evolution.

Recent molecular work has shown that arthropod development is under the control of clusters of *Hox* genes which regulate, directly or indirectly, large numbers of other genes (Akam *et al.* 1994; Carroll 1995; Carroll *et al.* 1995). *Hox* genes are highly conserved and originated before the divergence of the insect and crustacean lineages, probably not later than the Cambrian about 500 million years ago (Averof and Akam 1993). *Hox* genes determine positional identity along the body axis of arthropods. There is a striking correlation between the order of these genes on the chromosome and the position of their expression in the developing animal (Averof and Akam 1995a).

All the evidence to date supports the view that the generation of arthropod diversity has largely involved regulatory changes in the expression of conserved arrays of *Hox* genes and the evolution of interactions between Hox proteins and the genes they regulate (Carroll 1995). Thus if a particular segment has the potential to produce an appendage, the products of *Hox* genes can suppress this outcome, or even control the type of structure that develops from a range of alternatives. When the normal sequence of events is disrupted by homeotic mutation/malformation, the 'wrong type' of appendage can be produced. In Collembola, Fjellberg (1976b) described a specimen of *Proisotoma subarctica* on which an extra tenaculum (the

'catch' for the spring) developed on abdominal segment 2 in addition to the normal tenaculum on abdominal segment 3 (see Fig. 8.15).

Collembola occupy a position within Insecta on the phylogenetic 'trees' shown in Figs. 3.1 and 3.3, yet it remains to be seen whether these arrangements will survive in their present forms. What is needed urgently is molecular data on more species, both from the groups shown in Fig. 3.3, and those yet to be examined (especially Pauropoda, Symphyla, Protura and Diplura).

All data, molecular, morphological and ecological (Fjellberg 1976*d*; Miller and Wenzel 1995) should be examined by strict logical cladistic methodology to produce the most parsimonious cladogram (Wägele 1994; Wägele and Wetzel 1994). A statement of the current situation would have to say that Collembola are a monophyletic group within Insecta, probably a basal branch off the stem from which Euinsecta developed (Fig. 3.1), but that their exact position is still unclear. These are exciting times for invertebrate evolutionary biologists.

3.2.2 *Rhyniella praecursor* and other ancient Collembola

Direct fossil evidence of Collembola before the Devonian is lacking (Lehmann and Hillmer 1983). However, the recent discovery of coprolites (fossil faeces) in Upper Silurian rocks of 412 million years (Myr) in age, which could be derived from springtails (Edwards *et al.* 1995), suggests that Collembola were an important component of the earliest terrestrial ecosystems. A comprehensive list of fossil Collembola is given by Carpenter (1992).

The earliest fossil 'hexapod' (and possibly the most famous fossil insect) is *Rhyniella praecursor* Hirst and Maulik 1926 (Fig. 3.4). About 15 specimens have been discovered to date in Lower Devonian chert (400 Myr) from Rhynie, near Aberdeen in Scotland (Whalley and Jarzembowski 1981). This species has been placed in a variety of families including Rhyniellidae (Paclt 1956), Protentomobryidae (Salmon 1964), Neanuridae (Delamare Deboutteville and Massoud 1967; Massoud 1967*a*), and Isotomidae (Greenslade and Whalley 1986).

When one examines the cut and polished rock slices of *Rhyniella praecursor* held in the Natural History Museum in London, the similarity of the specimens to modern-day Collembola is striking. Entognathous mouthparts are present (see Fig. 3.4) and at least one specimen has a structure resembling a furca. The remarkable state of preservation of the material has led to the ancient status of the chert being questioned (see Greenslade 1988 for a detailed rebuttal). However, Devonian plant fragments are embedded in the chert and argon dating has proved their great age (Whalley 1995). The Isotomidae is probably the most acceptable family in which to place *Rhyniella* at the moment (Greenslade and Whalley 1986). However, there seems to be at least one more species present in the chert (possibly a member of the Neanuridae, Greenslade personal communication) but a definitive opinion on its taxonomic position cannot be given until more specimens are discovered and examined.

Far better preserved are springtails in amber (Fig. 3.5). Amber is fossilised resin of trees that lived millions of years ago. Animals which became stuck in the resin have retained their structure in superb detail (Poinar 1992, 1993). The collection at

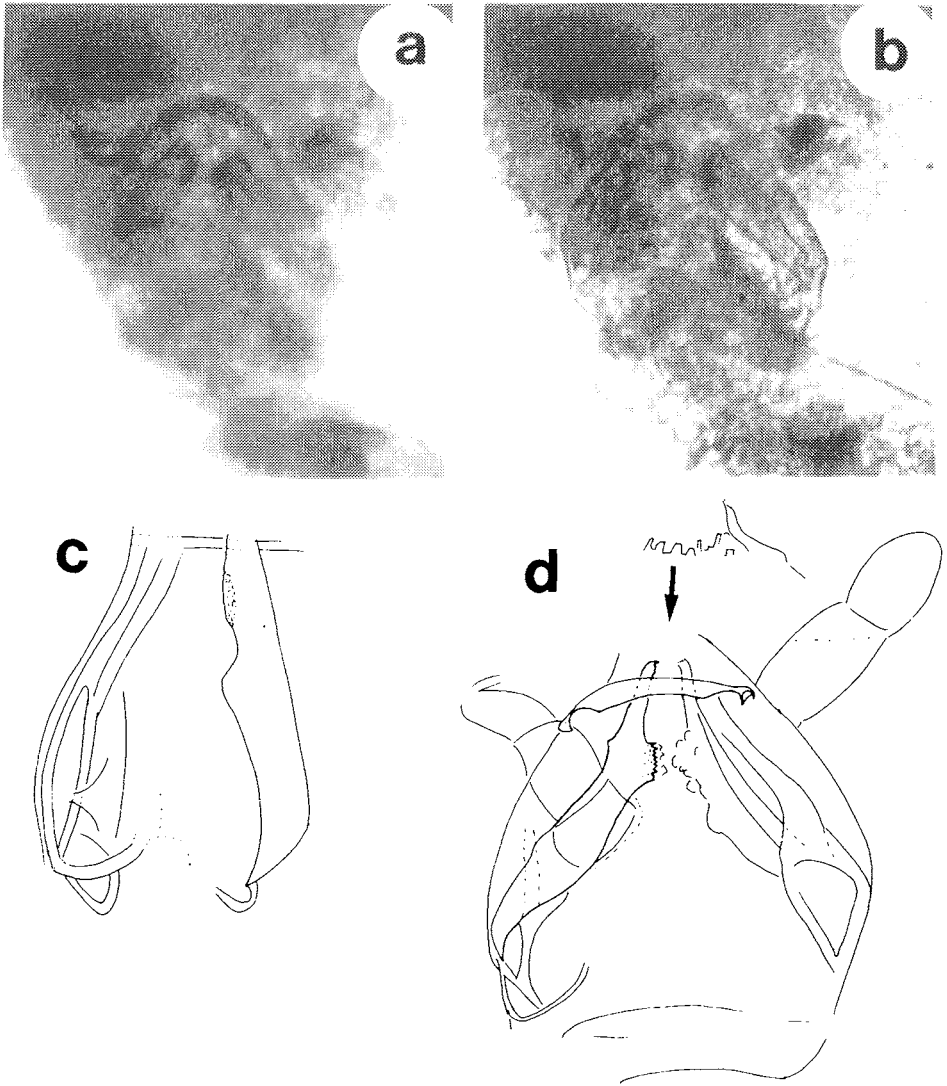


Fig. 3.4. *Rhyniella praecursor*. (a, b) Photographs of the mouthparts embedded in Rhynie Chert of 400 million years in age (Natural History Museum, London, specimen 38225). (c,d) Drawings of the mouthparts of the same specimen. Reproduced from Greenslade and Whalley (1986) by kind permission of the authors and the University of Siena.

the Natural History Museum in London contains several items of exquisite jewellery at the heart of which are pieces of amber containing beautifully preserved animals, some of which are now extinct. Where more than one species is present, the amber may provide evidence of community structure (Pike 1994), and interactions such as phoresy and predation (Poinar 1992).

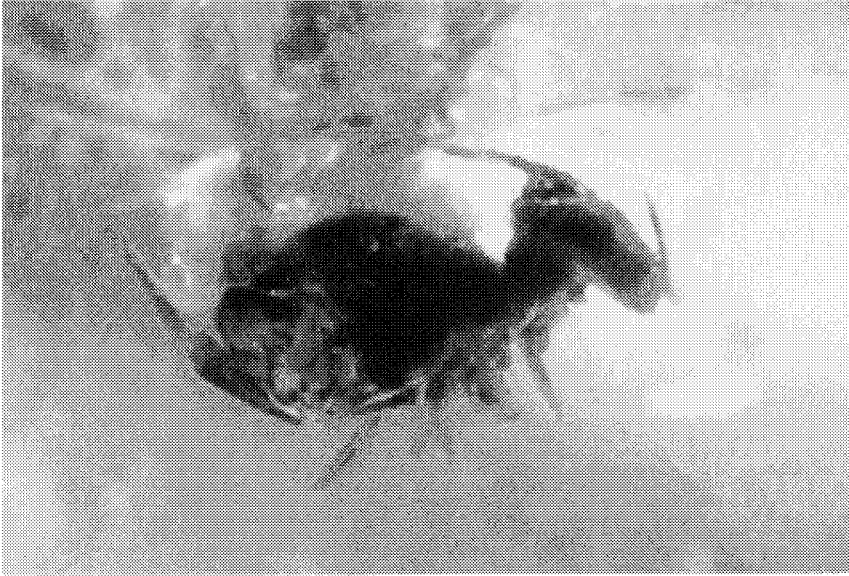


Fig. 3.5. Sminthurid springtail (1 mm in length) preserved in Baltic Amber of 40 million years in age. Photograph by Steve Hopkin (Natural History Museum, London, specimen II 558(1)).

The oldest springtail in amber is *Protentomobrya walkeri* Folsom 1937 from Cretaceous deposits in Manitoba, Canada (Delamare Deboutteville and Massoud 1968). This has traditionally been placed in its own family Protentomobryidae, although Greenslade and Whalley (1986) have suggested that it may be a member of the Isotomidae. What is remarkable about later Collembola in amber is their similarity to present day species (Keilbach 1982). All the well-preserved specimens observed in Miocene amber (*ca.* 30 Myr) from Mexico by Christiansen (1971*b*) and from Dominica by Mari Mutt (1983*b*) could be assigned to extant genera. Some 43% of Mari Mutt's specimens belonged to *Lepidocyrtus* and *Seira*.

3.2.3 Collembola in early terrestrial ecosystems

The majority of springtails in amber are those that climbed trees. Nevertheless, this limited evidence suggests that most communities of Collembola have probably been stable for tens of millions of years, punctuated by periods of rapid speciation when new niches became available (Gould and Eldredge 1993). The lack of fossil evidence makes it difficult to reconstruct early evolution. However, there are clues which allow a tentative scenario to be proposed as to how springtails colonised the land from an as yet unknown marine ancestor.

Molecular evidence (see Section 3.2.1) suggests that this ancestor was possibly a crustacean-like, multisegmented animal. During the Cambrian, these creatures colonised mats of algae and cyanobacteria in the littoral zone and in river estuaries where they fed on fungal hyphae and lichens (Gray and Shear 1992; Little 1990; Price 1988; Pritchard *et al.* 1993; Shear 1992*b*; Shear and Kukalová-Peck 1990).

Over many millions of years they became progressively more terrestrial (Vannier 1983, 1987a). It is unlikely that the 'protocollembolan' was ever a large animal (there are few modern day springtails more than 10 mm in length) but it *would* be nice to find a fossil collembolan of similar proportions to gigantic early millipedes which reached nearly 2 m (Hopkin and Read 1992).

The following events are some of the adaptations to land that may have taken place during the evolution of Collembola from a hypothetical many-legged, crustacean-like ancestor (not necessarily in this order).

- The second antennae were lost as they were no longer needed for swimming (reduction of one of the two pairs of antennae has also occurred in oniscidian isopods or woodlice in their transition onto land).
- The number of segments was reduced until only the head and the three thoracic and six abdominal segments remained.
- The legs on the thoracic segments were retained. However, those on the fourth abdominal segment were modified to form the jumping organ or furca by fusion of the basal parts (manubrium) leaving only the dens and mucro separate (see Fig. 4.1).
- The legs on the third segment were reduced and became the tenaculum or 'catch' for the furca.
- Those on the first abdominal segment developed thinly-walled vesicles and evolved into the ventral tube (see Fig. 6.4).
- Legs were suppressed on the second, fifth and sixth abdominal segments.

As land plants evolved and became progressively taller and more diverse (Edwards and Selden 1992), Collembola radiated to fill the new niches that became available. A layer of leaf litter provided a stable moist environment and many species moved permanently into the soil where the jumping organ, pigment and eyes were no longer needed and were lost. Others moved into the trees where they became among the most abundant arthropods in forest canopies (Betsch *et al.* 1980).

It is likely that the majority of families that we recognise today had evolved by the time *Rhyniella* was jumping over the surface of primeval swamps during the Devonian period 400 million years ago. However, more fossil and molecular evidence is needed before the full picture of the evolution of Collembola and other insects can be painted.

3.3 Systematics of the Class Collembola

It is now accepted almost universally that all formal categories of classification should be monophyletic i.e. the organisms within each must be derived from a single common ancestor. There seems little doubt that the Class Collembola is a monophyletic group. Autapomorphies which support this view are the possession of a ventral tube and a springing organ or furca (secondarily lost in some species). However, classification schemes such as that presented in Table 3.1 still use

Table 3.1. Classification of the Class Collembola

1. Order Arthropleona		
1.1	Superfamily Poduroidea (= Poduromorpha)	
1.1.1	Family Brachystomellidae	(96 spp.)
1.1.2	Family Hypogastruridae	
1.1.2.1	Subfamily Gulgastrurinae	(1 sp.)
1.1.2.2	Subfamily Hypogastrurinae	(577 spp.)
1.1.2.3	Subfamily Isotogastrurinae	(2 spp.)
1.1.3	Family Neanuridae	
1.1.3.1	Subfamily Capitanurinae	(7 spp.)
1.1.3.2	Subfamily Frieseinae	(148 spp.)
1.1.3.3	Subfamily Morulinae	(17 spp.)
1.1.3.4	Subfamily Neanurinae	(606 spp.)
1.1.3.5	Subfamily Pseudachorutinae	(367 spp.)
1.1.3.6	Subfamily Uchidanurinae	(15 spp.)
1.1.4	Family Odontellidae	(100 spp.)
1.1.5	Family Onychiuridae	
1.1.5.1	Subfamily Onychiurinae	(427 spp.)
1.1.5.2	Subfamily Pachytullbergiinae	(3 spp.)
1.1.5.3	Subfamily Tetrodontophorinae	(4 spp.)
1.1.5.4	Subfamily Tullbergiinae	(168 spp.)
1.1.6	Family Poduridae	(1 sp.)
1.2	Superfamily Entomobryoidea (= Entomobryomorpha)	
1.2.1	Family Actaletidae	(9 spp.)
1.2.2	Family Coenaletidae	(2 spp.)
1.2.3	Family Cyphoderidae	(123 spp.)
1.2.4	Family Entomobryidae	
1.2.4.1	Subfamily Entomobryinae	(1130 spp.)
1.2.4.2	Subfamily Orchesellinae	(235 spp.)
1.2.5	Family Isotomidae	(1028 spp.)
1.2.6	Family Microfalcuidae	(1 sp.)
1.2.7	Family Oncopoduridae	(40 spp.)
1.2.8	Family Paronellidae	(336 spp.)
1.2.9	Family Tomoceridae	(115 spp.)
2. Order Neelipleona		
2.1	Family Neelidae	(25 spp.)
3. Order Symphypleona		
3.1	Family Mackenziellidae	(1 sp.)
3.2	Family Sminthuridae	
3.2.1	Subfamily Bourletiellinae	(176 spp.)
3.2.2	Subfamily Dicyrtominae	(161 spp.)
3.2.3	Subfamily Katianninae	(241 spp.)
3.2.4	Subfamily Sminthuridinae	(126 spp.)
3.2.5	Subfamily Sminthurinae	(181 spp.)
3.2.6	Subfamily Spinothecinae	(4 spp.)
3.2.7	Subfamily Sturminae	(1 sp.)

Linnaean categories which may be difficult to adapt to a strictly cladistic analysis of evolutionary relationships (Bretfeld 1994a; Queiroz and Gauthier 1994).

The freedom to construct radical arrangements of taxa is limited to some extent by the requirements of the International Code for Zoological Nomenclature (Jeffrey 1989). While this has been essential for sorting out problems of synonymy, there is

currently a vigorous debate on whether strict adherence to the articles of the ICZN is constraining modern classification (for an excellent summary of current views see Minelli 1993). Most of the families and subfamilies shown in Table 3.1 probably *are* monophyletic groups. Nevertheless, the classification should be regarded for the moment as a convenient arrangement rather than the most parsimonious solution to the problem of how to subdivide the Class Collembola. Thus, families and subfamilies are presented in alphabetical order to reflect the uncertainties of their true relationships. The genera of the large family Isotomidae are given in alphabetical order in Appendix A since there is some disagreement as to the subfamilies into which they should be placed. I have not included tribes for similar reasons.

The arrangement of families and subfamilies used in this book is based on those of Greenslade (1991a, 1994a). I have followed her suggestion that Dicyrtomidae (*sensu* Greenslade 1994a) should 'perhaps be more correctly treated as a subfamily of the Sminthuridae following Richards (1968)'. In general, the lower the taxonomic level, the more the controversy. Most disagreements tend to be at the species or genus levels (Chapter 5). Indeed it is remarkable how few differences exist between the current arrangement of families (Table 3.1) and those used in the early part of this century (e.g. Shoenbotham 1917). Most changes have been due to raising subfamilies to family status, rather than moving taxa between these categories.

Several attempts have been made to reconstruct the evolution of Collembola (Cassagnau 1971a; Massoud 1976; Paclt 1956; Salmon 1964; Uchida 1971; Yosii 1961). Nevertheless, a convincing phylogenetic tree has not yet been established (Greenslade 1991a). For example, Moen and Ellis (1984) considered that *Podura aquatica* (see Fig. 3.6d) is so unlike other members of the Poduroidea that it should be placed in its own category Metaxypleona as the sister group of Neelipleona + Symphypleona. The sister group of the 'Poduromorpha' which have a well-developed prothorax (perversely now without *Podura aquatica*) are those Collembola with a reduced prothorax i.e. 'Entomobryomorpha' + Metaxypleona + Neelipleona + Symphypleona. This argument has not received wide acceptance, so I have retained the more traditional arrangement where the Class Collembola is divided into three Orders (see Table 3.1).

Genetic sequences have been elucidated in very few species of springtails (Friedrich and Tautz 1995; Hwang *et al.* 1995; Soto-Adames *et al.* 1994). The 18S rDNA sequences of *Hypogastrura* 'sp.' (Hypogastruridae) and *Crossodonthina koreana* (Neanuridae) were shown to be very similar by Hwang *et al.* (1995). However, it has not yet been discovered whether this is because the two families are closely related, or is due simply to these particular genes in springtails being highly conserved. It remains to be seen whether molecular evidence will be able to clarify relationships between the different families of Collembola. An overview of the systematic methods that have been used for studying the taxonomy of Collembola is given by Prabhoo (1987).

3.4 Families of Collembola (Table 3.1)

A complete list of world genera of Collembola is given in Appendix A. The following brief account gives an overview of each family. The Poduroidea (Sections

3.4.1–3.4.6) contains those families in which the most anterior segment of the thorax (prothorax) is obvious and always bears at least a few dorsal setae. Much use is made of the structure of the mouthparts in separating the families. Poduroidea tend to be slow-moving Collembola and most dwell in soil or under stones, bark, or leaf litter. Some have lost the ability to jump. The Entomobryoidea (Sections 3.4.7–3.4.15) tend to be more active springtails with a greatly reduced prothoracic segment (which never bears dorsal setae) and greater ability to jump. The Neelipleona comprises a single family Neelidae (Section 3.4.16) of small blind soil-dwellers which are globular in shape. The Symphypleona (Section 3.4.17) are also globular in shape with fused abdominal segments (the largest can be mistaken for small aphids with the naked eye). Many of the Symphypleona have considerable jumping ability and are common on above-ground vegetation and among trees in tropical countries.

3.4.1 *Brachystomellidae* (96 species)

This family used to be considered a subfamily of Neanuridae but is now regarded by most authors as being sufficiently distinct for family status. The most characteristic feature is the complete absence of mandibles (Adams and Salmon 1972). Fourteen genera are known, by far the largest of which is *Brachystomella* with 61 species described to date. The family has a worldwide distribution and includes the common and widespread species *Brachystomella parvula* (Fig. 3.6a).

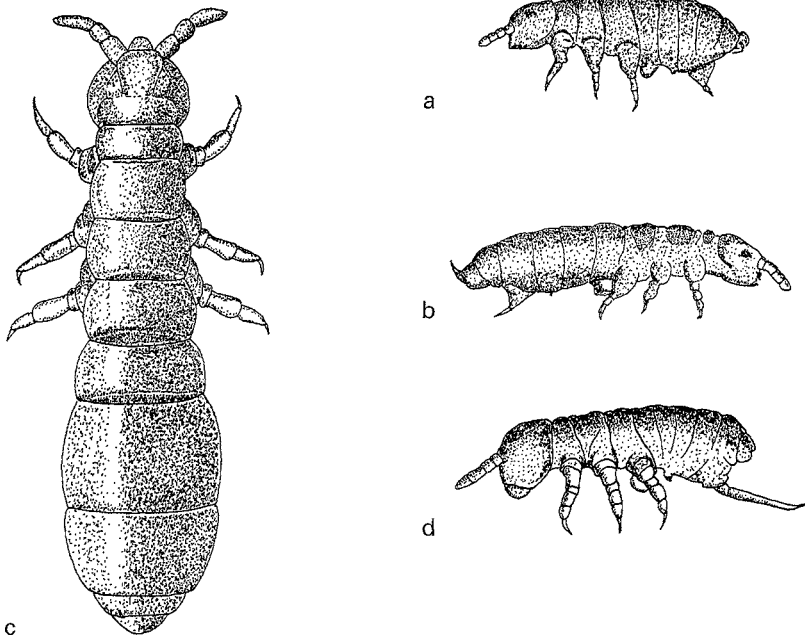


Fig. 3.6. (a) *Brachystomella parvula* (Brachystomellidae) of 1 mm in length. (b) *Hypogastrura* sp. (Hypogastruridae : Hypogastrurinae) of 2 mm in length. (c) *Anurida maritima* (Neanuridae : Pseudachorutinae) of 3 mm in length. (d) *Podura aquatica* (Poduridae) of 2 mm in length. Note that in live specimens, the furca is normally held pointing forwards against the abdomen. Based on Gisin (1960a), Imms (1906) and Pomorski and Skarzynski (1992).

Brachystomellids are mostly confined to damp soil although some genera and species are associated with fungal fruiting bodies (Greenslade 1994a).

3.4.2 Hypogastruridae (580 species)

The Hypogastruridae consists of two very small subfamilies, Gulgastrurinae (one species from Korean caves) and Isotogastrurinae (two species from littoral habitats in the West Indies and Canary Islands), and one very large subfamily, the Hypogastrurinae, with a cosmopolitan distribution. The positions of Gulgastrurinae and Isotogastrurinae are by no means certain but they are placed here tentatively as they seem closer to hypogastrurids than to other Collembola. There are 577 species of Hypogastrurinae in 39 genera. A mandibular plate is present on the mandible (see Fig. 4.5b) and the maxilla has a stout cardo between the stipes and fulcrum (see Fig. 4.5e). The largest genera are *Ceratophysella* (102 species), *Hypogastrura* (136 species; Fig. 3.6b), and *Xenylla* (125 species). Members of the Hypogastrurinae are found in numerous habitats including soil, under bark, the seashore, commercial mushroom beds and the percolating filters of sewage treatment works where they can be extremely abundant. Members of this subfamily are those most often found in huge 'swarms'.

3.4.3 Neanuridae (1160 species)

This is one of the most intensively studied and diverse families of Collembola characterised by the absence of the mandibular plate (see Fig. 4.5c,d), and maxilla with long slender cardo between the stipes and the fulcrum (Deharveng 1982a, 1983a; Massoud 1967b; Fig. 4.5g). These are possibly derived characters from a 'hypogastrurid-like' ancestor (for an attempt at a cladistic analysis of Neanuridae, see Lee 1985b). Six subfamilies are recognised which are described briefly below. However, relationships within Neanuridae are not clear and the arrangement presented here may not be a natural one (Fjellberg 1985c). Most neanurids are found under bark and stones and within soil or leaf litter where they feed on fungal hyphae and other foods which they pierce with their mouthparts. The salivary glands of some species are large and may contain giant chromosomes (see Figs. 5.5, 5.6).

The Capitanurinae is a small subfamily (seven species in two genera) of very small orange, blue or grey springtails which are known only from Korea where they occur under stones and rotting wood (Lee 1983a; Najt and Weiner 1992). They have a very flattened body, no furca and a most unusual appearance due to the dorsoventral 'migration' of the head and posterior abdomen (Fig. 3.7).

The Frieseinae contains 148 species in two genera, 147 of which are in the cosmopolitan genus *Friesea*. They are characterised by the structure of the mouthparts which are adapted for feeding on rotifers (Deharveng and Bedos 1991), other Collembola (Christian 1989a) and their eggs (Petersen 1971a). *Friesea mirabilis* is found under stones and in leaf litter and is one of the most widespread species.

The Morulininae is represented by only one genus *Morulina* with 17 species found in North America, Europe and southeast Asia (Bödvarsson 1960a;

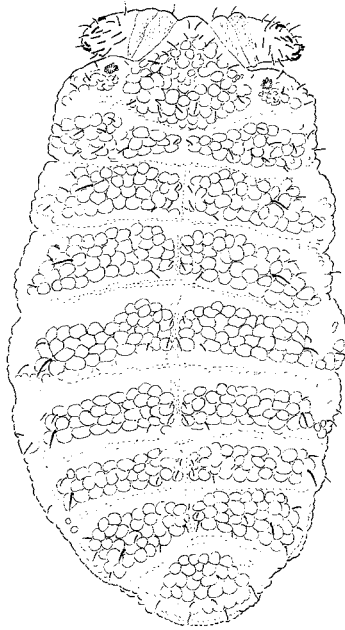


Fig. 3.7. *Caputanurina nana* (Neanuridae : Caputanurinae) of 0.5 mm in length from Korea. Reproduced from Lee (1983a) by kind permission of the author and the *Korean Journal of Entomology*.

Deharveng and Weiner 1984) and Japan (Tanaka 1984). All species have a post-antennal organ of distinct structure and five ocelli on each side of the head. Some are covered in long blunt spines (Fig. 3.8).

The largest and best-studied members of the Neanuridae are the Neanurinae comprising 606 species in 87 genera. While some species such as *Neanura muscorum* occur all over the world, most genera are endemic to particular regions (Cassagnau 1988), particularly southeast Asia where considerable adaptive radiation has occurred. Cassagnau, Deharveng and others have described numerous new genera and species in this subfamily (Appendix A) and there may be many more species waiting to be discovered. *Paralobella orousseti*, from Luzon Island in the Philippines, is perhaps the most beautifully coloured of all springtails with its transverse bands of yellow, red and white pigment (Cassagnau and Deharveng 1984). The 'body plan' of this group has clearly been a very successful evolutionary development (Deharveng 1984b). Cassagnau (1982, 1983a,b, 1989) gives detailed summaries of probable evolutionary relationships of the different lineages of Neanurinae.

The Pseudachorutinae (367 species in 44 genera) includes the diverse and widespread genera *Pseudachorutes* (85 species) and *Anurida* (68 species). *Anurida maritima* (see Fig. 3.6c) is one of the most abundant invertebrates in northern temperate littoral habitats.

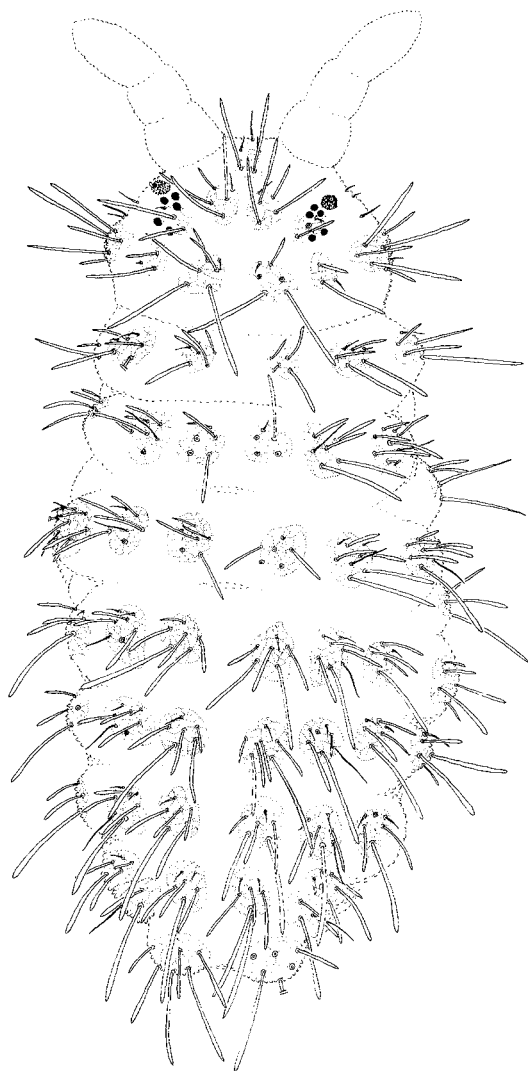


Fig. 3.8. *Morulina pawlowskii* (Neanuridae : Morulininae) of 2.5 mm in length from North Korea. Reproduced from Deharveng and Weiner (1984) by kind permission of the authors and Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Université Paul Sabatier, Toulouse.

The Uchidanurinae (15 species in eight genera) was established by Cassagnau (1980*b*). Its members are among the largest and most spectacularly-coloured of all Collembola reaching up to 10 mm in length and bearing elongate digitations or lobes (Fig. 3.9) which may be tipped with red, orange or yellow pigment (Greenslade 1991*b*; Massoud 1964*a*). Uchidanurids are associated with decaying logs in temperate and subtropical rainforests (Greenslade 1994*a*). They occur in two quite separate geographical regions, one encompassing N.E. India, Malaysia,

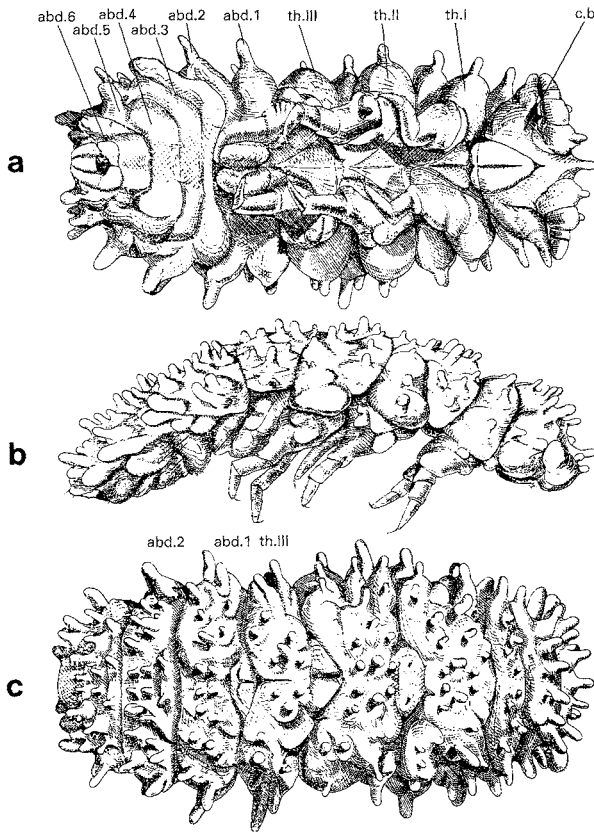


Fig. 3.9. *Caledonimeria mirabilis* (Neanuridae : Uchidanurinae) from New Caledonia. (a) Ventral view, (b) side view and (c) dorsal view. Reproduced from Vannier and Najt (1991) by kind permission of the authors and Editions Gauthier-Villars.

Indochina and Borneo and the other comprising the Marquesas, New Caledonia (Vannier and Najt 1991), New Zealand, S.E. Australia and Tasmania. Greenslade (1991*b*) has stressed the conservation importance of this subfamily and the vulnerability of the endemic genera, particularly in Australia.

3.4.4 Odontellidae (100 species)

Odontellidae (100 species in 13 genera) was established as a family by Deharveng (1981*a*) and is now widely accepted (Fjellberg 1995*a*; Greenslade and Deharveng 1984). Deharveng concluded that the Odontellidae had evolved independently from the lineage Hypogastruridae/Neanuridae/Brachystomellidae, mainly on the basis of the structure of the mouthparts in which the cardo is 'displaced', and stipe and fulcrum articulate directly (see Fig. 4.5f). Most of the Odontellidae have antennae with a pronounced conical shape and a furca with two lobes on the

micro. The largest genera are *Odontella* with 22 species confined to the 'austral' region (S. America, Australia, New Zealand) and *Superodontella* with 48 species (raised from subgenus to genus level by Bedos and Deharveng 1990) with a cosmopolitan distribution.

3.4.5 Onychiuridae (602 species)

Members of this family are leaf litter or soil-dwelling forms in which pigment, eyes and a jumping organ are almost always absent (see Figs. 5.12, 5.13). They possess defensive pores called 'pseudocelli' which are small areas of thin cuticle through which defensive fluid can be extruded (see Section 4.2.4; Fig. 4.11). Most species are small and white but *Tetrodontophora bielanensis* (of the distinctive subfamily Tetrodontophorinae) can reach 9 mm in length and is blue-grey in colour. The Onychiuridae have been the subject of intense taxonomic study and there has been substantial 'splitting' of genera and species (reviewed in depth for Onychiurinae in Section 5.4). In Appendix A, I have followed the eclectic approach of Christiansen and Bellinger and have included all the genera on their list, although some taxonomists consider them to be of subgenus status only.

The three monospecific genera of Pachytullbergiinae are of uncertain position within the Poduroidea. In spite of possessing some onychiurid-like characters (Rusek 1976), Pachytullbergiinae are thought by Deharveng (personal communication) to be an artificial grouping.

Tullbergiinae has been subjected to substantial 'splitting' in recent years and it is difficult to present a list of genera which every taxonomist would accept. The characters on which some genera are founded are subtle and there are undoubtedly more re-arrangements to come (Fjellberg 1991c; Lucianez and Simon 1992b,d, 1993a; Rusek 1986a; Weiner and Najt 1991a). Members of the Onychiurinae and Tullbergiinae are distributed widely throughout the world, a few transported by human activity from their original localities (Greenslade 1994a).

3.4.6 Poduridae (1 species)

The single species in this family, *Podura aquatica* (see Figs. 2.3, 3.6d), is among the most common springtails in the Northern Hemisphere. During the summer months, it can be found in large numbers in sheltered corners of streams, freshwater ditches and ponds (Pichard 1973). *P. aquatica* has a holarctic distribution and was thought by Moen and Ellis (1984) to be the sole survivor of one of the original stems of collembolan evolution. Its taxonomic position is by no means certain (Section 3.3) as it shares some characteristics with the Arthropleona (Dallai and Malatesta 1973) and others with Symphypleona and Neelipleona. However, presence of a haploid chromosome number in *P. aquatica* of $n = 11$ (the highest of any springtail) compared to typically $n = 5$ in Symphypleona makes a close relationship between these two taxa questionable (Hemmer 1990). Molecular evidence would be useful in order to clarify the relationship of *P. aquatica* to other families of Collembola.

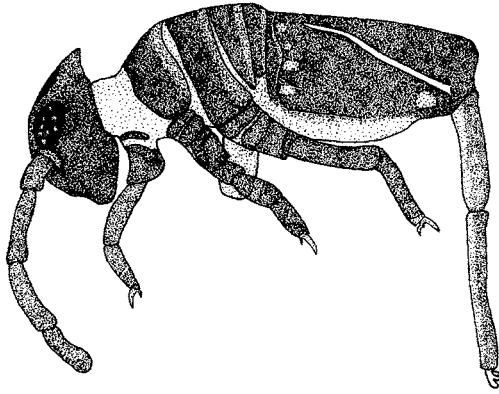


Fig. 3.10. *Spinactaletes myoptesimus* (Actaletidae) of 1 mm in length from Puerto Rico. Reproduced from Soto-Adames (1988b) by kind permission of the author and the College of Arts and Sciences, University of Puerto Rico, Mayagüez.

3.4.7 Actaletidae (9 species)

All species of Actaletidae are rare and are strictly marine littoral (see Delamare Deboutteville 1964 for a discussion of earlier descriptions of *Actaletes*). This small family has been revised recently by Soto-Adames (1988b) who erected the genus *Spinactaletes* (Fig. 3.10) to distinguish the eight species from Jamaica, Venezuela, Puerto Rico and Mexico from the single species *Actaletes neptuni* that is confined to Europe. Actaletidae are alone among Arthropleona in possessing tracheae. Formerly placed in Isotomidae by Gisin (1960a), their position as a family within Entomobryoidea is likely to be revised in the light of further taxonomic work and the description of new species which are sure to be discovered.

3.4.8 Coenaletidae (2 species)

This family established by Bellinger (1985a) contains two species, *Coenaletes vangoethemi* from Papua New Guinea (originally placed in *Actaletes*) and *Coenaletes caribaeus* from Guadeloupe in the Caribbean. Both species are commensal with hermit crabs. Coenaletidae share similarities with Isotomidae and Actaletidae but like the latter, their present taxonomic position may be revised in the light of new discoveries.

3.4.9 Cyphoderidae (123 species)

This is an interesting family of 13 genera, formerly considered to be a subfamily of Entomobryidae, but now given family status by most authors (Greenslade 1994a; Yoshii 1980, 1987, 1992b). All species occur in the nests of bees (Mari Mutt 1977), ants or termites (Section 7.3.3), and are blind and poorly-pigmented. The largest genus *Cyphoderus* (60 species) is worldwide but others are more local, their distribution limited presumably by that of their host species of hymenopteran or termite.

3.4.10 *Entomobryidae* (1365 species)

This is a huge family divided into two subfamilies which in total contain 21% of all described species of Collembola. They can be found throughout the world in a wide range of habitats but most species live among leaf litter, on the soil surface, on and under the bark of trees, in the forest canopy, or in caves (see Fig. 9.14d). The Entomobryinae (1130 species) contains 41 genera and are characterised by having the fourth abdominal segment larger than the third, and antennae with four segments. In contrast, the Orchesellinae (235 species; Mari Mutt 1980) has 14 genera in which the third and fourth abdominal segments are more or less equal in size, with some antennal segments subdivided. For example, in *Orchesella cincta* the first two antennal segments are divided giving a total of six sections (see Fig. 2.5) whereas in *Heteromurus nitidus*, only the first segment is subdivided giving a total of five sections.

The boundaries of species in the largest genera of the Entomobryinae are in many cases not clearly defined. In *Entomobrya* (217 species) and *Pseudosinella* (247 species, many of which are cave-dwelling) there is probably synonymy still to be resolved. Attempts have been made by Yoshii to split the large genus *Lepidocyrtus* (185 species). However, some of the characters used by Yoshii may be paraphyletic (Christiansen and Bellinger personal communication) so a broad definition of *Lepidocyrtus* is retained for the present in Appendix A.

3.4.11 *Isotomidae* (1028 species)

The Isotomidae may be an early branch off the path leading to the 'higher' Entomobryomorpha. The abdominal segments are all of similar length and most species live in soil, in crevices on the seashore, or associated with freshwater. *Isotomurus palustris* is one of the most widespread and frequently-recorded springtails and can invariably be found among marginal vegetation of ponds and streams. Members of this family are found throughout the world, some in extreme habitats such as deserts (Suhardjono and Greenslade 1994), and others in the Antarctic where *Cryptopygus antarcticus* (see Frontispiece and photograph in Schaller 1992) is among the most abundant of all invertebrates.

Parthenogenetic *Folsomia candida* (see Fig. 10.1) are used widely by ecotoxicologists in a standard test for assessing the effects of chemicals on non-target soil invertebrates (Chapter 10).

3.4.12 *Microfalculidae* (1 species)

The single species in this family, *Microfalcula delamarei* (Fig. 3.11), has been found only in Madagascar where it may be commensal in the nests of termites (Betsch and Massoud 1973; Massoud and Betsch 1966a,b). Its affinities are unclear but it is probably closest to the Entomobryidae within Entomobryomorpha. However, further specimens need to be collected before its position can be ascertained with confidence.

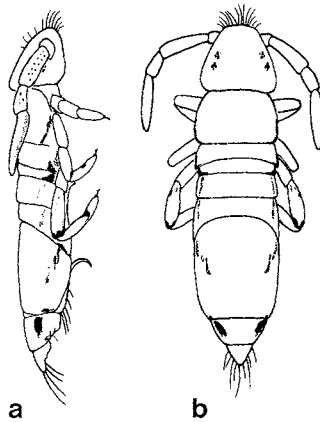


Fig. 3.11. *Microfalculla delamarei* (Microfalculidae) of 1 mm in length from Madagascar. (a) Side view, (b) dorsal view. Reproduced from Massoud and Betsch (1966b) by kind permission of the authors and Editions Gauthier-Villars.

3.4.13 *Oncopoduridae* (40 species)

This small family comprises two genera, *Harlomillsia* with one species (*H. oculata*) known from the USA, Mexico, Japan, the Philippines, Thailand and Indonesia, and *Oncopodura* (39 species) of wider distribution (Deharveng 1988d; Szeptycki 1977b). All are rare soil- or cave-dwelling forms (Christiansen and Reddell 1986). Szeptycki (1977a) placed Oncopoduridae close to Tomoceridae based on similarities in the structure of cuticular scales and body chaetotaxy.

3.4.14 *Paronellidae* (336 species)

Paronellidae is the only major family of Collembola whose members do not occur in most northern temperate latitudes (the northern limit for *Salina* in North America is Indiana; Bellinger personal communication). However, paronellids can be found on glaciers in Australia and New Zealand (Greenslade personal communication), so the reasons for their restricted distribution remain a mystery. They are characterised by having very long antennae, furca and fourth abdominal segment (see Fig. 9.14e). Some paronellids are brightly coloured such as the yellow and purple *Campylothorax melanocephalus* which lives in riparian rain forests in Zaire (see colour photograph in Mitra and Dallai 1980). Most species live on trees, shrubs, epiphytes, grasses or in superficial layers of leaf litter (Greenslade 1994a). However, some of the 24 genera are found only in caves and these may exhibit reductions in pigmentation, number of ocelli on the head, and length of appendages (Deharveng and Gers 1993; Palacios-Vargas and Wilson 1990; Wilson 1982). Paronellids are particularly diverse in tropical rain forests (Yoshii and Greenslade 1993).

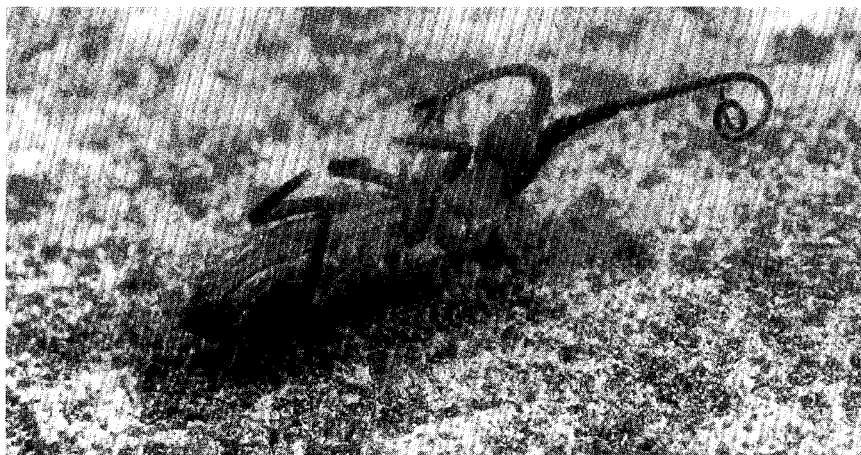


Fig. 3.12. *Pogonognathellus longicornis* (Tomoceridae) of 6 mm in length from Reading, UK. The specimen was repeatedly made to jump until it became motionless with fatigue (it recovered after about 10 min and was able to walk away). The animal's left antenna is coiled (cf. Fig. 2.4) but the fourth section of the right antenna is reduced in length, presumably due to an earlier attack by a predator. Photograph by Steve Hopkin.

3.4.15 Tomoceridae (115 species)

This family includes some of the most widespread and common springtails of the holarctic region although a few genera can be found in the Southern Hemisphere (Ireson and Greenslade 1990). *Pogonognathellus longicornis* (formerly *Tomocerus longicornis* but see Massoud and Ellis 1974) is very familiar to North European workers and is probably the same species as *Podura plumbea* listed by Linnaeus in the tenth edition of *Systema naturae* (see Fig. 2.2). Members of Tomoceridae have a third abdominal segment which is only slightly longer than the fourth, and antennae in which the third segment is longer (sometimes much longer) than the fourth. This enables some species to roll the antennae into a coil (see Figs. 2.4, 3.12). A major review of the Tomoceridae was published by Yosii (1967a).

Several of the 47 species in the largest genus *Tomocerus* are separated on the basis of quite subtle differences in the morphology of the mucro at the end of the furca, and the foot claws (Christiansen 1964b). I have found these characters to be quite variable within populations of what are undoubtedly the same species and there are likely to be some cases of synonymy waiting to be uncovered. Some species are found in caves (Christiansen 1980) and exhibit reductions of pigment and number of ocelli (see Fig. 9.14c).

3.4.16 Neelidae (25 species)

Members of this cosmopolitan and poorly studied family are quite common in collections of springtails extracted from soil with Tullgren funnels, but are often overlooked due to their minute size. Neelidae are sufficiently different in structure from all other springtails to be assigned to their own Order Neelipleona

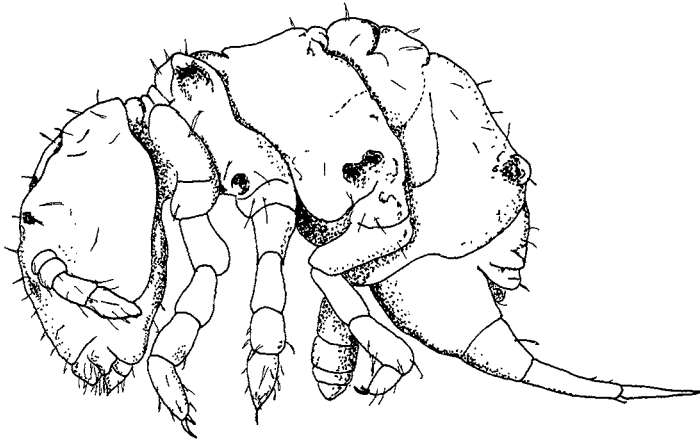


Fig. 3.13. *Megalothorax minimus* (Neelidae) of 0.4 mm in length. Redrawn from Börner (1906b).

(Blancquaert and Mertens 1979; Massoud 1971). The Neelidae (Fig. 3.13) bear a superficial resemblance to Sminthuridae but differ in that the globular body is formed largely by expansion of the thoracic rather than abdominal segments (Moen and Ellis 1984). All species live in soil or in caves (Deharveng and Beruete 1993), are blind, and have very short antennae (Börner 1906a; Dallai 1979b).

3.4.17 *Mackenziellidae* (1 species)

The first specimens of the single species within this family *Mackenziella psocoides* (Fig. 3.14) were found by Marie Hammer in Northern Canada in 1948 (Hammer 1953). It has since been found in Germany, Norway and the Canary Islands (Fjellberg 1989). All records are from moss in dry situations in which *Mackenziella psocoides* can be locally abundant. However, it is extremely small (only 0.25 mm in length) and has probably been overlooked over a much wider geographical range. Fjellberg (1989) has put forward convincing arguments that Mackenziellidae are a branch off the Sminthuridae line and should be included in Symphypleona. Males have clasping organs on the antennae (Fig. 3.14e) and both sexes have lost the mandibles and maxillary outer lobe. The elongate body and prognathous head are probably an adaptation for penetrating the narrow spaces between moss leaves in search of food particles.

3.4.18 *Sminthuridae* (890 species)

Representatives of this large and cosmopolitan family are among the most frequently encountered and brightly coloured springtails. They live predominantly in superficial leaf litter, on low vegetation, on the surface of still fresh water, and are abundant on trees, particularly in the canopies of tropical humid forests. Sminthuridae have a characteristic globular shape formed by the enlargement and fusion of posterior thoracic and anterior abdominal segments (see Figs. 2.1, 2.6, 3.15). Most species are exceptional jumpers and some have a conspicuous ventral

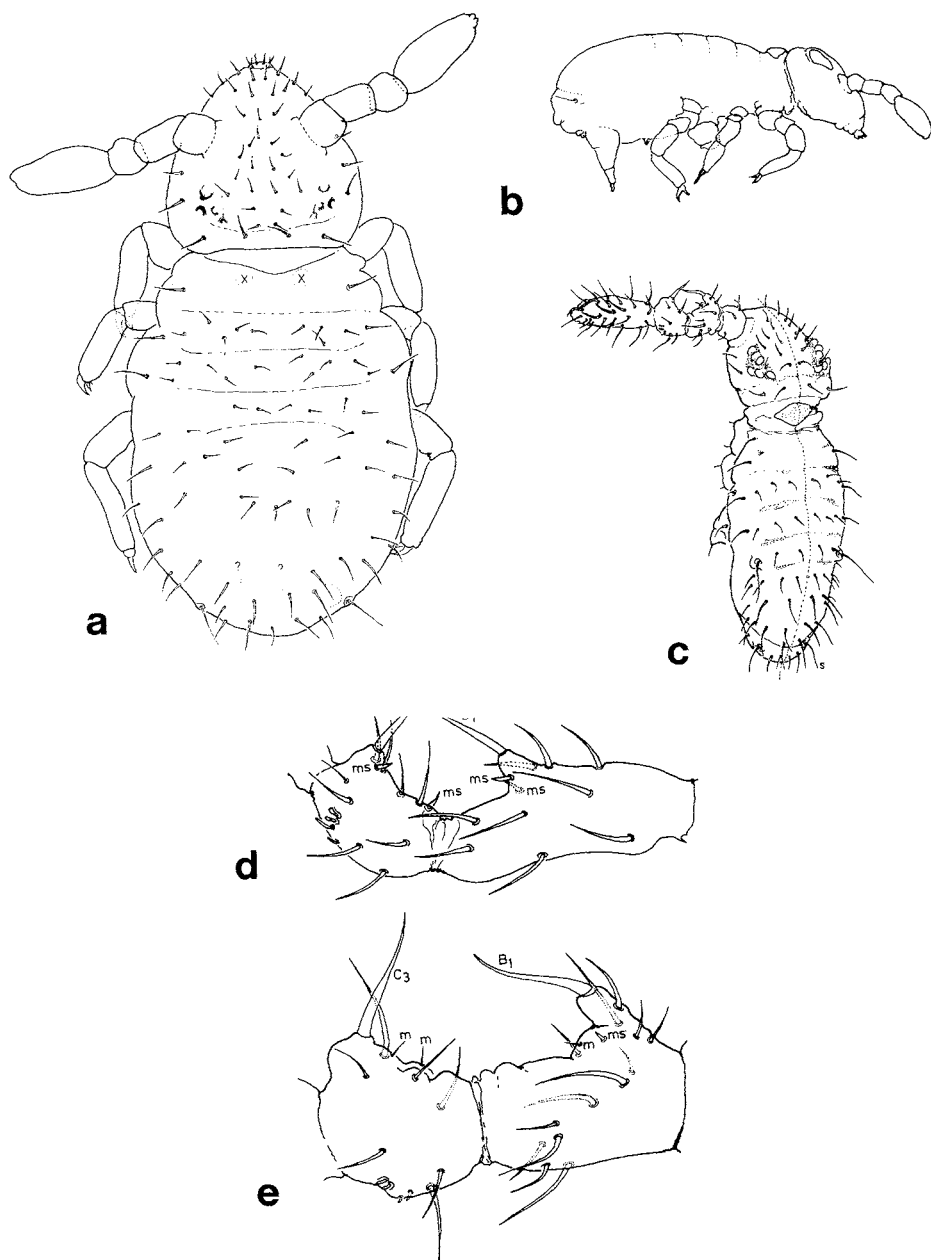


Fig. 3.14. *Mackenziella psocoides* (Mackenziellidae). (a) Dorsal and (b) side view of a female specimen of 0.25 mm in length from Northern Canada. (c) Lateral view of a male of 0.18 mm in length (right antenna and legs not shown). (d) Male clasp organ on the antenna of *Sphaeridia* sp. (Sminthuridae), (e) male clasp organ on the antenna of *Mackenziella psocoides* from Tenerife. Reproduced from Fjellberg (1989) by kind permission of the author and the University of Siena (a and b originally from Hammer 1953).

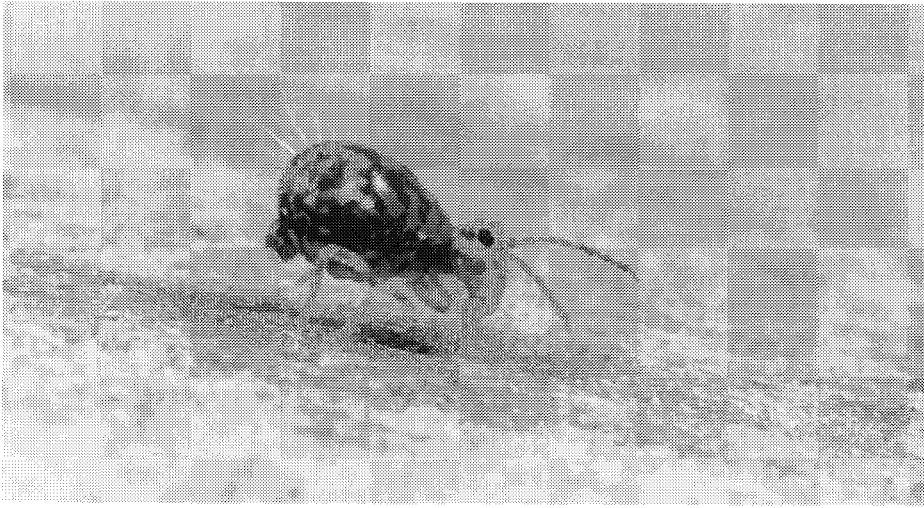


Fig. 3.15. *Dicyrtomina ornata* (Sminthuridae : Dicyrtominae) of 1.5 mm in length from Reading, UK. Photograph by Steve Hopkin.

tube, the vesicles of which when extruded, extend for more than twice the length of the body (Section 4.2.1).

The distribution of genera between the categories of Sminthuridae is derived largely from the excellent and comprehensive monographs of Richards (1968) and Betsch (1980). Phylogenetic analysis of the Symphypleona relies to some extent on differences in patterns of setae on the head, thorax, abdomen and appendages ('chaetotaxy', see Section 5.2.4), but there is currently a debate on how such information should be interpreted (Bretfeld 1986*b*, 1990, 1992*a,b*; Nayrolles and Betsch 1993). Other characters include the structure of the furca, antennae and features in the vicinity of the anus and genital opening. In the summary below, I have followed a conservative line by retaining Sminthuridae as a family, and have used the subfamilies as defined in the list of Christiansen and Bellinger on which Appendix A is based.

The Bourletiellinae (176 species in 22 genera) occur in the Northern Hemisphere, the tropics and Australia. Several species have been introduced to areas south of the Equator (Greenslade 1994*a*). The Bourletiellinae includes the widespread and familiar species *Bourletiella hortensis* whose mating 'dance' between male and female was so lovingly described by Lubbock (1873, page 109, under the name *Smynturus luteus*; Section 8.3.3). The leaves of the peonies (*Paeonia officianalis*) in my garden in Reading are covered in dozens of these springtails during the summer months (see Fig. 8.5).

Greenslade (1994*a*) and others have treated the Dicyrtominae (161 species in seven genera) as a distinct family. However according to Richards (1968) this is 'unsupportable as many structures are intermediate between Katianninae and Sminthurinae'. Despite this, one morphological feature easily separates dicyrto-

mids from the other Symphyleona; the fourth antennal segment is always less than one half the length of the third (see Fig. 3.15). Although widespread, the subfamily is predominantly Oriental (Greenslade 1994a).

Katianninae (241 species in 17 genera) are widespread but are found mainly in the Southern Hemisphere. All species are small (less than 1.5 mm in length) and possess a trochanteral organ on the legs of the metathoracic segment. The Subfamily includes the genera *Arrhopalites* and *Collophora* some of which are cave species with reduced eyes and pigment (Christiansen 1966; Fig. 9.14a). These two genera have been allocated to their own family Arrhopalitidae by some authors (e.g. Betsch 1980).

The most characteristic feature of the Sminthurinae (126 species in ten genera) is their sexual dimorphism (Betsch and Massoud 1970). In the males, the antennae are strongly modified for clasping the female during mating (Fig. 8.4) and the females lack anal appendages. These rather small springtails (most are less than 1 mm in length) are distributed throughout the world and are often found on the surface of water.

The Sminthurinae (181 species in ten genera) are found mainly in the Northern Hemisphere and the tropics. The common species *Sminthurus viridis* (Fig. 2.6), which is native to the Northern Hemisphere, has been transported to several countries including Australia where it is an important economic pest of clover (hence its colloquial name of the 'Lucerne flea'; Section 7.5). The pantropical genus *Temeritas* includes species with the largest antennae of any sminthurid collembolan; the fourth segment has a large number of subsegments and the total length of the antennae may exceed twice the length of the body (Betsch 1971; Dallai and Fanciulli 1985).

Spinothercinae is a small subfamily found in cool temperate forests that contains only four described species in two genera (Greenslade 1982b). *Adelphoderia regina* is confined to Australia. Of the remaining species in the genus *Spinotherca*, one occurs in New Zealand and two in South America. The subfamily is characterised by the presence of a pair of unusual tubular organs encircling the neck. These are filled with haemolymph and may function as sites of gas exchange (Greenslade 1982b).

Sturmiinae (as Sturmiidae) was erected by Bretfeld (1994a) for the single species *Sturmius epiphytus* from epiphytic mosses and ferns in Columbian mountain forest. This species appears to be close to the Katianninae but is placed here in its own subfamily for the present owing to its enigmatic taxonomic position.

3.5 Biogeography

3.5.1 Introduction

Biogeography is the branch of biology concerned with the distribution of plants and animals. Knowledge of distribution is particularly important for setting priorities for conservation (called the 'agony of choice' by Vane-Wright *et al.* 1991). However, habitats that are 'centres of biodiversity' are not necessarily rich in

species of all taxa (Prendergast *et al.* 1993). As far as Collembola are concerned, there is no substitute for designated fieldwork by experts at identification if one is to be certain of the global distribution and hence rarity of each species.

3.5.2 Continental drift and speciation

About 200 million years ago, all the continents were joined together in the super-continent of Pangea. The 'northern' continents separated from Pangea leaving Gondwanaland which began to break up about 180 million years ago into the present-day continents of South America, Africa, India, Antarctica, and Australia and New Zealand (Storey 1995). All the main families of Collembola had almost certainly evolved before the break up of Pangea and Gondwanaland (Rapoport 1971). One of the aims of biogeographers is to be able to interpret the present day distribution of taxa in the light of continental drift (Blackith and Blackith 1975).

The movements of the continents and appearance of new mountain ranges and oceanic islands provided numerous new habitats for Collembola to colonise. Considerable adaptive radiation took place in some of these areas manifested most clearly by the large number of endemic species and genera found on isolated islands and mountains (Cassagnau 1981, 1988, 1991*a,b*, 1993*a,c*; Dallai 1983; Deharveng 1980*b*, 1981*d*; Deharveng and Bedos 1993*b*; Fjellberg 1992*b*; Lee and Kim 1990; Thibaud 1991*a*; Thibaud and Najt 1993). Of the 47 species of Collembola known from Antarctica, 70% are endemic to the continent (Block 1984*a*).

Some quite widespread genera have undergone adaptive radiation following geographic isolation. For example, Deharveng and Bedos (1991) concluded that every mountain of tropical Asia above 2000 m is likely to yield endemic species of the widespread genus *Friesea*.

3.5.3 Dispersal and migration

Four processes add or subtract species from a region:

- speciation
- extinction
- biotic dispersion
- long-distance dispersal (Cracraft 1994).

In the case of Collembola, biotic dispersion is by walking (or jumping). Long-distance dispersal may be by the wind, birds, clinging to sea surface debris carried on ocean currents, or human activities. Thus a single geographical region may contain a mixture of cosmopolitan, locally distributed and apparently endemic species (Stomp *et al.* 1982). Furthermore, species may become locally extinct leaving 'gaps' in their distribution, or completely extinct as has probably occurred to many species of springtails in Hawaii (Christiansen and Bellinger 1992, 1994).

It is a major problem to elucidate the geographic origin of each species within a region, and the date of first colonisation. Attempts have been made to determine

the original localities of the ancestors of species that occur on oceanic islands. One of the most detailed studies was that of Gama (1986a) who listed probable origins of the Collembola of the four main island groups of Macaronesia. It was clear that the springtails were derived from land masses on both sides of the Atlantic. Bellinger and Christiansen (1989), Christiansen and Bellinger (1992, 1994) and Snider (1990a) presented detailed arguments in support of the conclusion that the Collembola which colonised Hawaii before the arrival of humans, came from all the continents bordering the Pacific rim.

Human introductions are a major problem when trying to reconstruct evolutionary pathways of taxa, adaptive radiation events, and former land bridges between continents based on present day distributions. In earlier centuries, soil was commonly used as ballast in ships and was dumped overboard, or unloaded on the dockside to make space for cargo. Many plants were also transported between continents. The soil around their roots would have contained numerous soil organisms which were released into the environment when the plants were removed from their pots in their new home. Many species must have been transported via these routes from one side of the world to the other. Bellinger and Christiansen (1989) estimated that 64 of the 167 species of Collembola known from Hawaii had probably been introduced by humans.

3.5.4 *Present-day distribution of Collembola*

Recent checklists of species on a country by country basis are cited in Appendix B. However, national boundaries may cut across areas with similar climate or vegetation type. It is more relevant from a biological point of view to divide the world into biogeographical regions. Christiansen and Bellinger recognise 37 such areas of the world in their electronic list (available from the e-mail address given in Section 1.4) and for every species, give the regions from which they have been recorded. Thus it is very easy to ascertain the known distribution of every species in the world by consulting this list.

Collembola are under-recorded in comparison to more 'popular' arthropods such as butterflies and beetles. Many springtails are small and cryptically coloured and are easily overlooked by less-experienced collectors. Species that live permanently in soil may be difficult to find even if they have previously been found at a site. Thus a published map does not necessarily illustrate the true distribution of a species but represents the places collembologists have visited (Lawrence 1969b). Large and spectacularly-coloured springtails are less likely to be overlooked. Thus the disjunct distribution of the Uchidanurinae, which occur in two quite separate geographic regions (Section 3.4.3), is more likely to be a true picture than maps of the occurrence of tiny soil-dwelling species.

Numerous lists have been published of the localities where particular species have been found. Nevertheless, few attempts have been made to produce distribution maps of the geographical ranges of individual species such as that for *Tetracanthella arctica* by Samways (1994). 'Dot-distribution' maps are especially useful since they feature exact localities. There is also a considerable incentive for

fieldworkers to place a dot in a region from which the species has not previously been recorded. In Europe for example, such maps are available for *Disparrhopalites patrizii* (Dallai 1970a), and several sminthurids (Bretfeld 1989a,b) and neanurids (Cassagnau 1979). It is important to recognise that these maps give only a 'snapshot' of the known distribution. New discoveries may render conclusions obsolete. For example, maps produced by Dallai (1980b) and Selga (1966) appeared to suggest that *Proctostephanus madeirensis* was restricted to Madeira and Portugal. However, this species has been discovered in Britain (Lawrence and Khaloyan 1977) on waste tips and while probably an introduction, it can clearly survive and breed out of doors in more northern climes.

3.5.5 Biogeographical correlation

The boundaries of the ranges of species which have restricted distributions can sometimes be correlated with climatic conditions and vegetation type. This is true for example of some species of *Xenylla* in Australia (Gama and Greenslade 1981). Information on distribution can also be used to award species status to varieties within morphologically homogenous 'species groups'. For example, Wallace (1973) split a large collection of '*Sminthurus viridis*', into three species based on their colouration. These were *Sminthurus viridis*, *Sminthurus marmoratus* and *Sminthurus nigromaculatus*. Although all three are morphologically similar (and are difficult to separate after colours have faded in preservative), there are clear differences between them in the geographical ranges that they occupy within Europe supporting their status as distinct species.

Ecomorphology and anatomy

4.1 Introduction

Some branches of traditional zoology have studied the comparative anatomy of animals with little regard for the functions of the features being described, or the selective pressures that have made them evolve in a particular way. Specimens preserved in alcohol have sometimes been regarded as objects for description rather than once-living dynamic organisms whose anatomy, physiology and behaviour are tuned acutely to their environment. The modern approach puts the morphology of animals in an ecological, physiological and behavioural context (e.g. Eisenbeis 1989*a,b*; Faber 1991*a*; Massoud and Thibaud 1985; Palacios-Vargas and Vasquez 1988; Petersen 1980; Siepel 1994*a,b*) and aims to elucidate why certain structures have evolved, an approach that is sometimes called 'ecomorphology'. For example, it has been a puzzle as to why the scales which cover the cuticle of certain species of entomobryoidids are so easily removed. However, behavioural experiments in the laboratory have suggested that the ease with which the scales are shed enables springtails such as *Heteromurus nitidus* to detach themselves from the sticky mouthparts of predatory beetles (Bauer and Pfeiffer 1991).

Several attempts have been made to group Collembola into different ecomorphological 'life forms'. Gisin (1943) distinguished three types of springtails. *Euedaphic* species are permanent soil-dwellers, *hemiedaphic* species are found in superficial soil layers and leaf litter, and *epedaphic* (*atmobiotic*) species live at the surface and on vegetation. This scheme was accepted by Petersen (1980) in his review of the topic and is followed here. Eisenbeis and Wichard (1987) proposed an even simpler scheme in which springtails are divided into *epedaphic* and *euedaphic* life forms. *Epedaphic* species live on or above the ground and are typified by most of the Entomobryoidea and Symphypleona. Their body surface is pigmented (sometimes patterned), often covered with hairs and scales, and their furca, antennae and eyes are well-developed. In contrast, *euedaphic* species inhabit the lower soil layers and are typified by members of Onychiuridae. These are poorly-pigmented with reduced furca, eyes and antennae. Species of Collembola found only in caves often exhibit similar reductions in pigmentation and eyes (Section 9.6).

Such schemes are useful for giving a broad overview of the main ecomorphological types of Collembola. Nevertheless, there are many species which are difficult to fit into such broad groups. An alternative scheme is to divide Collembola on the basis of the particular aspect of their life style that one is study-

ing. Faber (1991a), for example, separated Collembola into feeding guilds, each of which consumed the same type of fungus.

- *Epigeic (epedaphic) fungus feeders* interact with fungal colonisation of fresh leaf litter with the potential for affecting decomposition rates.
- *Hemiedaphic fungus feeders* affect net mineralization and nutrient mobilization in fragmented leaf litter.
- *Euedaphic fungus feeders* have the potential to affect plant growth by interference with the establishment of mycorrhizae or nutrient uptake by the roots.

Siepel (1994a,b) used characteristics of the life histories of Collembola in his discussion of life forms and concluded that the classification adopted should depend on the objective of the experiment.

In this chapter, the external morphology (Section 4.2) and internal anatomy (Section 4.3) of Collembola are described, together with a review of the sensory organs which provide springtails with information on their external environment (Section 4.4). An account is also given of the structure and function of the furca which endows Collembola with the ability to jump over a distance of many times their body length within a fraction of a second (Section 4.5).

4.2 Morphology

4.2.1 Body plan

The body of Arthropleona is clearly divided into a head, a thorax with three segments, and an abdomen with six segments (Fig. 4.1). In Neelipleona and Symphypleona (see Figs. 3.13, 3.15), the primary structure is the same but some thoracic and abdominal segments have fused to give these springtails their characteristic globular appearance. The main external features of Collembola are described briefly below. The body and appendages are furnished with a range of sensory organs, the structure and function of which are discussed in Section 4.4.

The segmental origin of the head is demonstrated most clearly by the mouthparts (Section 4.2.2). From anterior to posterior there are six fused head segments:

- the labral segment
- the antennal segment
- the postantennal segment which is fused with the antennal segment
- the mandibular segment
- the maxillary segment
- the labial segment (Gullan and Cranston 1994).

The paired appendages on these segments are serially homologous with legs.

The antennae of Collembola consist of four basic segments which are richly endowed with sensory organs (Eisenbeis and Wichard 1987; Nayrolles 1991; Figs. 4.19, 5.9). In some species, one or more of the sections may be divided into subunits which give the antennae greater flexibility. The antennae may be very long in

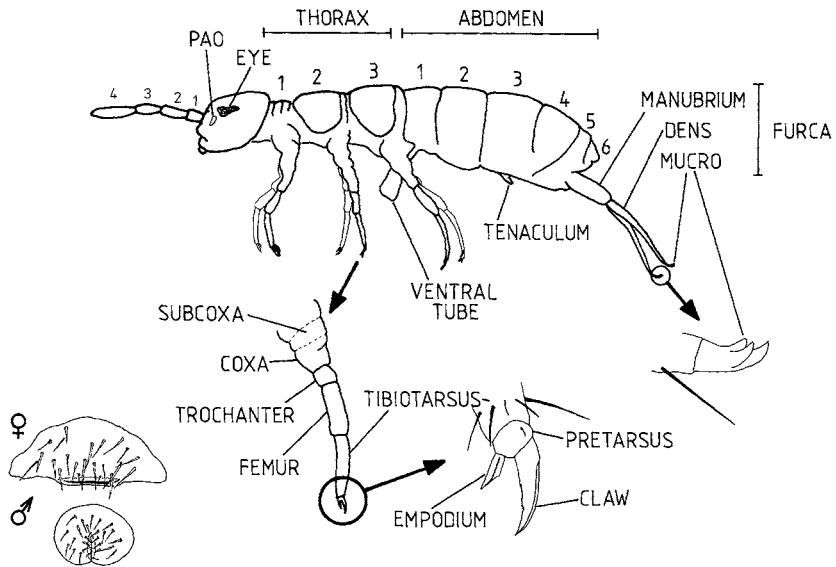


Fig. 4.1. *Isotoma viridis* (Isotomidae) of 4 mm in length showing the main morphological features of Collembola. In live specimens, the furca is normally held against the ventral side of the abdomen by the tenaculum. PAO, postantennal organ. Redrawn after various authors, mainly Fjellberg (1980a) and Gisin (1960a). The male or female genital plate is on the ventral side of the fifth abdominal segment. Those illustrated are of *Protaphorura aurantiaca* (Onychiuridae) after Pitkin (1980).

surface-dwelling Collembola (Goto 1955b). The Amazonian species *Mastigoceras camponoti* (Orchesellinae) for example has antennae which are more than three times the length of the body (Cassagnau and Oliveira 1992). In Mackenziellidae (Fjellberg 1989) and Sminthuridinae (Massoud and Betsch 1966c), the male antennae are modified for clasping the female during mating (Section 8.3). Antennal loss is very common in Collembola and is due mostly to attack from predatory beetles. However, a damaged antennae will grow back over several moults until it returns almost to its initial size (Ernsting and Fokkema 1983).

Each eye consists of a maximum of eight simple ommatidia (see Fig. 4.21). Some species are however completely blind. A postantennal organ is found in many species which may have an olfactory function (see Fig. 4.20).

The segments of the thorax each bear a pair of legs. Each leg is made up of a subcoxa, coxa, trochanter, femur, tibiotarsus and pretarsus with a claw and empodial appendage (see Fig. 4.1). The claws of some species are modified to enable them to walk more efficiently on wet surfaces (Deharveng and Gouze 1986; Fjellberg 1991a; Palévydy 1965). The tibiotarsus of others have one or more long 'tenant' hairs with sticky ends that allow these species to adhere to smooth surfaces (Blottner and Eisenbeis 1984).

The first segment of the abdomen of all Collembola bears a ventral tube which plays an extremely important role in fluid and electrolyte balance (Section 6.3.2; Fig. 6.4). The vesicles of the ventral tube when extruded may also be used for

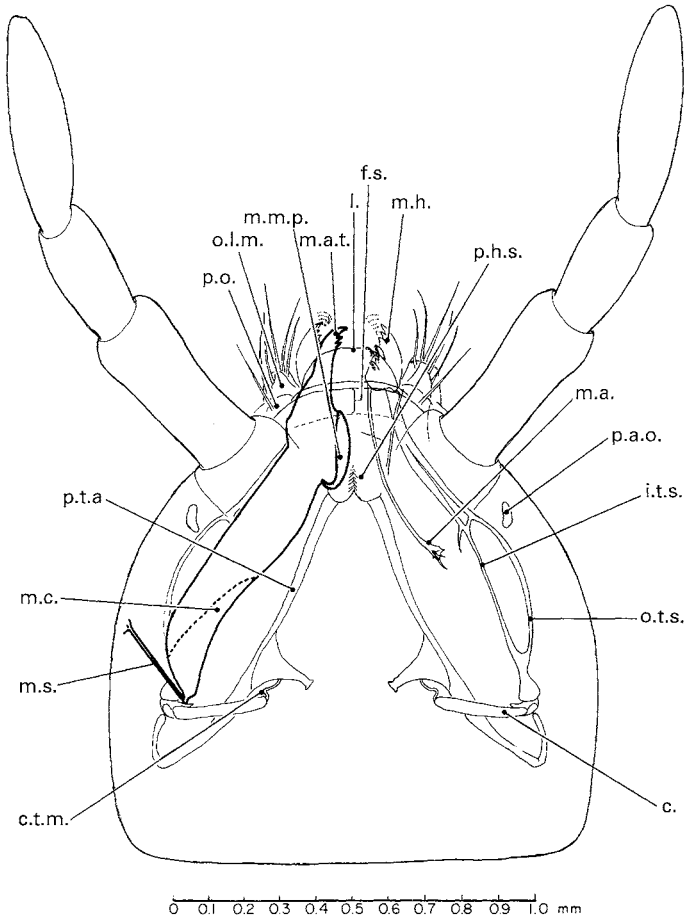


Fig. 4.2. Diagrammatic representation of the mouthparts and associated structures in dorsal view of *Folsomia candida* (Isotomidae). The mandible has been removed on the right side. c., cardo; c.t.m., cardo-posterior tentorial membrane; f.s., frontal sclerite; i.t.s., inner thickening of stipes; l., labrum; m.a., maxilla head apodeme; m.a.t., mandibular apical teeth; m.c., mandibular cavity; m.h., maxilla head (capitulum); m.m.p., mandibular molar plate; m.s., mandibular suspension; o.l.m., outer lobe of maxilla (maxillary palp); o.t.s., outer thickening of stipes; p.a.o., position of postantennal organ; p.h.s., position of hypopharynx and super linguae; p.o., *plica oralis*; p.t.a., posterior tentorial apodeme (fulcrum). Reproduced from Goto (1972a) by kind permission of the Linnean Society of London.

adhering to smooth surfaces, and as a source of 'grooming' fluid (Davies 1928b; Pedigo 1967). The ventral tube receives urine produced by the labial nephridia on the ventral side of the head via a groove called the *linea ventralis* (Rusek 1987b; Fig. 4.13). In Collembola which live in dry habitats, the groove is enclosed by cuticle to reduce evaporation (Verhoef *et al.* 1983).

The third segment of the abdomen bears the *tenaculum* (sometimes known as *retinaculum*) which functions as a 'catch' for the jumping organ or *furca* which

arises on the fourth abdominal segment. The structure and function of the 'spring' are covered in Section 4.5. The ventral side of the fifth segment bears the inconspicuous male or female genital opening (see Fig. 4.1). The end of the digestive tract opens via the anus on the sixth abdominal segment which bears three eversible sacs of unknown function (Leinaas 1988).

A number of other structures may be found whose function has not been elucidated. For example, the dorsal side of the fifth abdominal segment of species of the genus *Proctostephanus* (Isotomidae) bears a conspicuous 'crown' (Cassagnau 1953; Poinsoot and Dallai 1970).

4.2.2 Mouthparts

The mouthparts of Collembola develop within the buccal cavity of the head during embryogenesis (Uemiya and Ando 1987b). This *entognathy* is a characteristic feature of Collembola separating them from insects in which mouthparts are external and clearly visible. The basic structure of collembolan mouthparts is epitomised by *Folsomia candida* (Isotomidae), a species studied in detail by Goto (1972a) and on which the following account is based (Fig. 4.2).

The five main components of the mouthparts are the *labrum* (or 'upper lip'), a pair of *mandibles*, a pair of *maxillae*, the *hypopharynx* and the *labium* (Fig. 4.3). The *maxillary palps* are situated on each side of this complex. The mouthparts are enclosed dorsally by the labrum, ventrally by the labium and laterally by pleural folds of cuticle (Fig. 4.3). Each mandible bears a *molar plate* (Fig. 4.5a) which has traditionally been regarded as capable of grinding food although this has been dis-

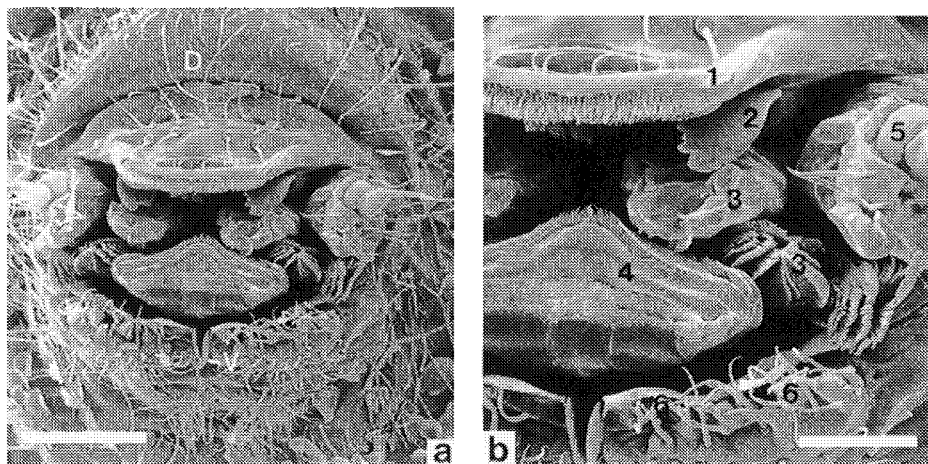


Fig. 4.3. Scanning electron micrographs of the mouthparts of *Pogonognathellus flavescens* (Tomoceridae) viewed from in front. (a) Low-power view. D, dorsal side of buccal cone; V, beginning of the ventral groove (cf. Fig. 4.13). Scale bar = 100 μ m. (b) Higher magnification view showing (1) labrum, (2) mandible, (3) maxilla, (4) hypopharynx, (5) maxillary palp and (6) labium. Scale bar = 50 μ m. Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

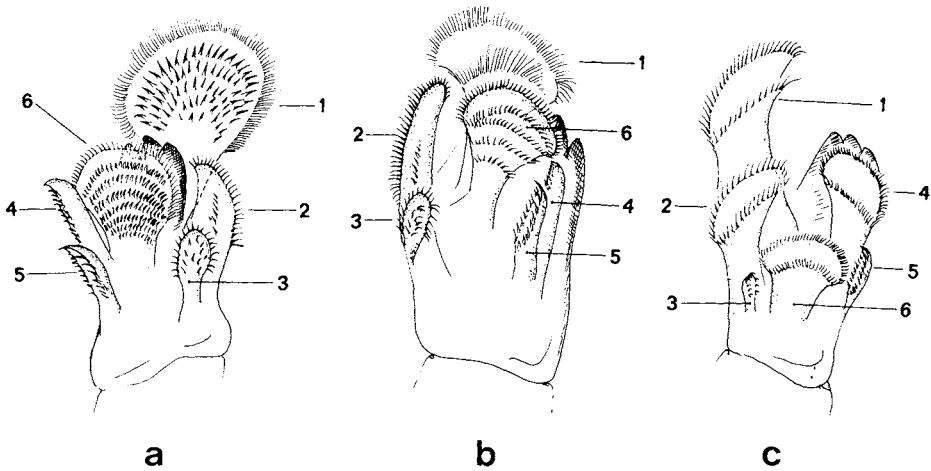


Fig. 4.4. Left maxilla of (a) *Isotoma notabilis* (Isotomidae), (b) *I. agrelli* and (c) *I. ekmani* showing the inner face as seen from the midline of the preoral cavity. Homologous lamellae are numbered 1–6. Reproduced from Fjellberg (1977b) by kind permission of the author and the Scandinavian Society for Entomology.

puted by Goto (1972a). The tips of the mandibles are however strongly toothed and are certainly capable of rasping a substrate to remove food material (Christian 1989a). Each maxilla bears a head or *capitulum* connected to a *stipe* which articulates via a *cardo* with a *fulcrum* (see Figs. 4.2, 4.5e). These structures are paired and the two fulcral arms converge anteriorly at the plate-like hypopharynx and its lateral lobes called *superlinguae*. The components of the cephalic endoskeleton are connected by muscles to tentorial projections on the internal surface of the head capsule to form the functional mouthparts (François and Chaudonnert 1982; Manton 1977). The fine structure of the mouthparts, and arrangements of setae on their components, are extremely important for the taxonomy of Collembola (Fjellberg 1976c, 1977b, 1984b,c; Figs. 4.4, 5.7).

The structure of the mouthparts in specific families may deviate substantially from this basic plan. Neanuridae have no molar plate on the mandibles (Fig. 4.5c,d,g) and feed by piercing and sucking their food (Petersen 1971a; Singh 1970). Brachystomellidae have no mandibles at all and feed by ingesting food particles in liquid suspension (Adams and Salmon 1972). Odontellidae are characterised by reduction of the cardo and direct articulation of the stipe and fulcrum (Deharveng 1981a; Fig. 4.5f). The Arctic collembolan *Metisotoma grandiceps* (formerly *Cephalotoma*) has asymmetric interlocking mandibles probably related to its carnivorous diet (Cassagnau 1972a).

4.2.3 Structure of the cuticle

The surface structure of the cuticle of Collembola is one of their most striking features in the scanning electron microscope (Fig. 4.6). The basic pattern is a hexagonal arrangement of triangular granules with linear connections between

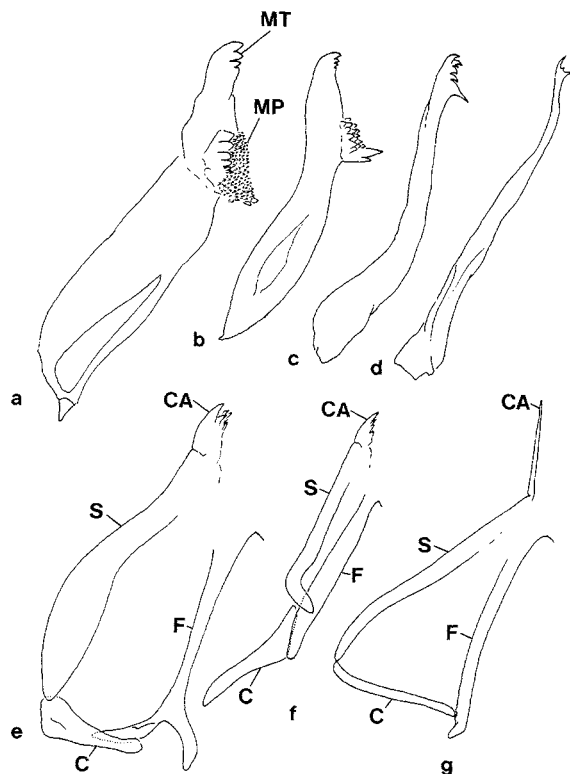


Fig. 4.5. Mandible of (a) *Tetracanthella pyrenaica* (Isotomidae), (b) *Willemia anophthalma* (Hypogastruridae), (c) *Yuukianura* sp. (Neanuridae) and (d) *Neanura muscorum* (Neanuridae). Maxilla of (e) *Ceratophysella tergilobata* (Hypogastruridae), (f) *Superodontella* sp. (Odontellidae), (g) *Deutonympha deficiens* (Neanuridae). C, cardo; CA, capitulum; F, fulcrum; MP, mandibular plate; MT, mandibular 'teeth'; S, stipe. Reproduced from Deharveng (1983a) by kind permission of the author and of Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Université Paul Sabatier, Toulouse.

(Massoud and Barra 1980; Fig. 4.7). These may be reduced to give a relatively smooth surface (Lawrence and Massoud 1973), or they may merge and enlarge to form secondary granules, or protuberances (Cassagnau and Lauga-Reyrel 1985; Dallai 1973b; Deharveng 1980a; Hale and Smith 1966; Harris 1979; Lawrence 1975; Lee 1983a; Massoud 1969; Massoud and Betsch 1973; Massoud and Thibaud 1979; Rosciszewska 1985). In species at risk from desiccation, the granules are closely apposed and the cuticle is thickened to lower its permeability and reduce transpiration of water (Cassagnau 1993a; Cassagnau and Lauga-Reyrel 1984; Harrisson *et al.* 1990, 1991; Mitra and Dallai 1980). However, adaptations of the arrangement of the granules to cold do not seem to occur (Eisenbeis and Meyer 1986). The internal structure of the cuticle is shown in Figs. 4.7 and 4.8.

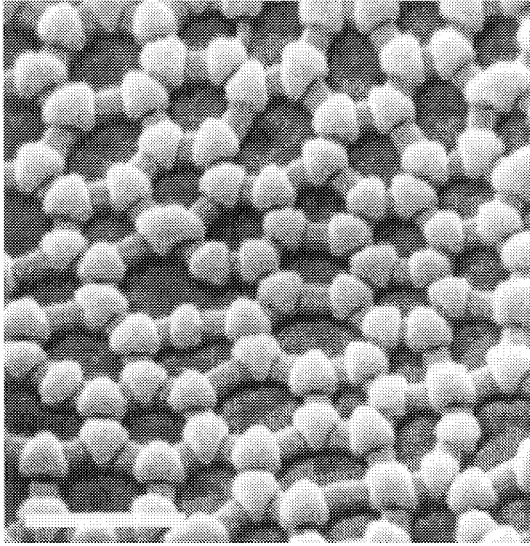


Fig. 4.6. Scanning electron micrograph of cuticle of *Pogonognathellus flavescens* (Tomoceridae) consisting of primary triangular granules (microtubercles) linked together in hexagonal 'rings'. Scale bar = 1 μ m. Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

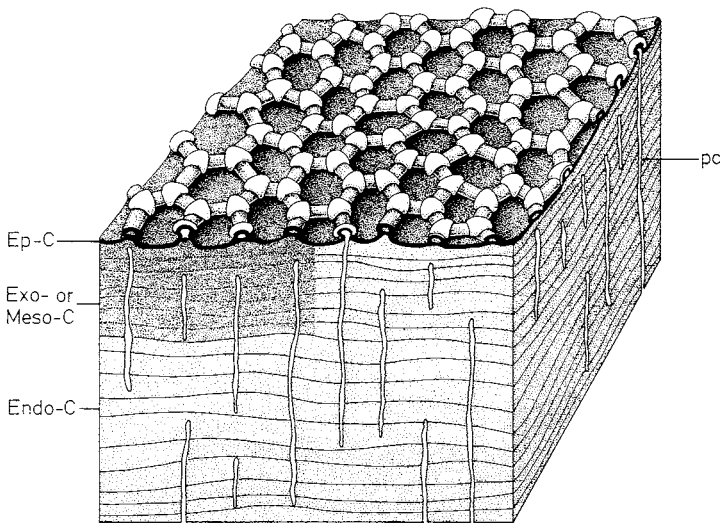


Fig. 4.7. Schematic diagram of the collembolan cuticle. Ep-C, epicuticle; Exo-, exocuticle; Meso-C, mesocuticle; Endo-C, endocuticle. The pore canals (pc) cross the lamellae of the cuticle ending in the microtubercles. Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

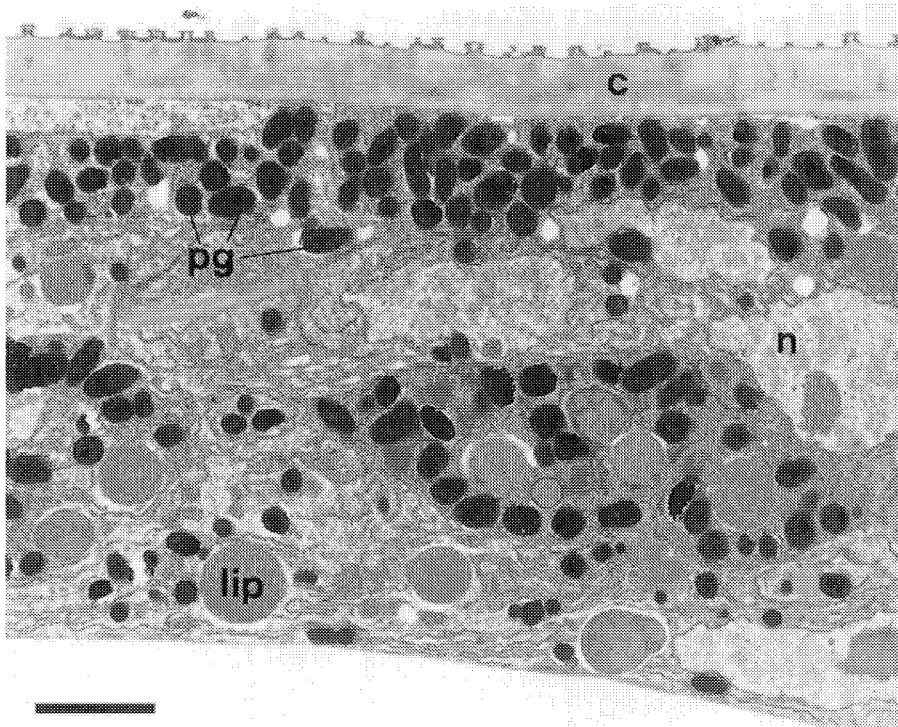


Fig. 4.8. Transmission electron micrograph of a section through the epidermis of *Isotoma* sp. (Isotomidae). c, cuticle; lip, lipid droplets; n, nucleus; pg, pigment granules. Scale bar = 2 μ m. Reproduced from Eisenbeis and Meyer (1986) by kind permission of the authors and the University of Siena.

The cuticle of most species is hydrophobic due to the presence of a waxy layer (Ghiradella and Radigan 1974). If this is removed with solvents, the cuticle becomes wettable (Noble-Nesbitt 1963a). In some Sminthuridae such as *Ptenothrix atra*, wax is secreted by specialised glands on the abdomen and stands proud of the cuticle in long blunt spines (Juberthie and Massoud 1977; Massoud and Vannier 1965a). In *Megalothorax minimus* (Neelidae), which also secretes wax, the 'wax spines' are secreted at a rapid rate taking only a few minutes to reach twice the body length (Vannier and Massoud 1967).

When submerged in water, springtails may continue to exchange gases with the external medium if a layer of air is retained against the body surface (Krzysztofowicz *et al.* 1972). King *et al.* (1990) provided convincing evidence for the presence of plastrons on the littoral springtails *Anuridella marina* and *Anurida maritima* which allow these Collembola to continue to respire when submerged (Fig. 4.9). Many neanurids have cavities between the epidermal cells and the cuticle which may also function in respiration (Lauga-Reyrel 1986).

The appearance of the cuticle in the scanning electron microscope has been used for taxonomic purposes (Dallai 1970b, 1974b, 1977; Dallai and Malatesta

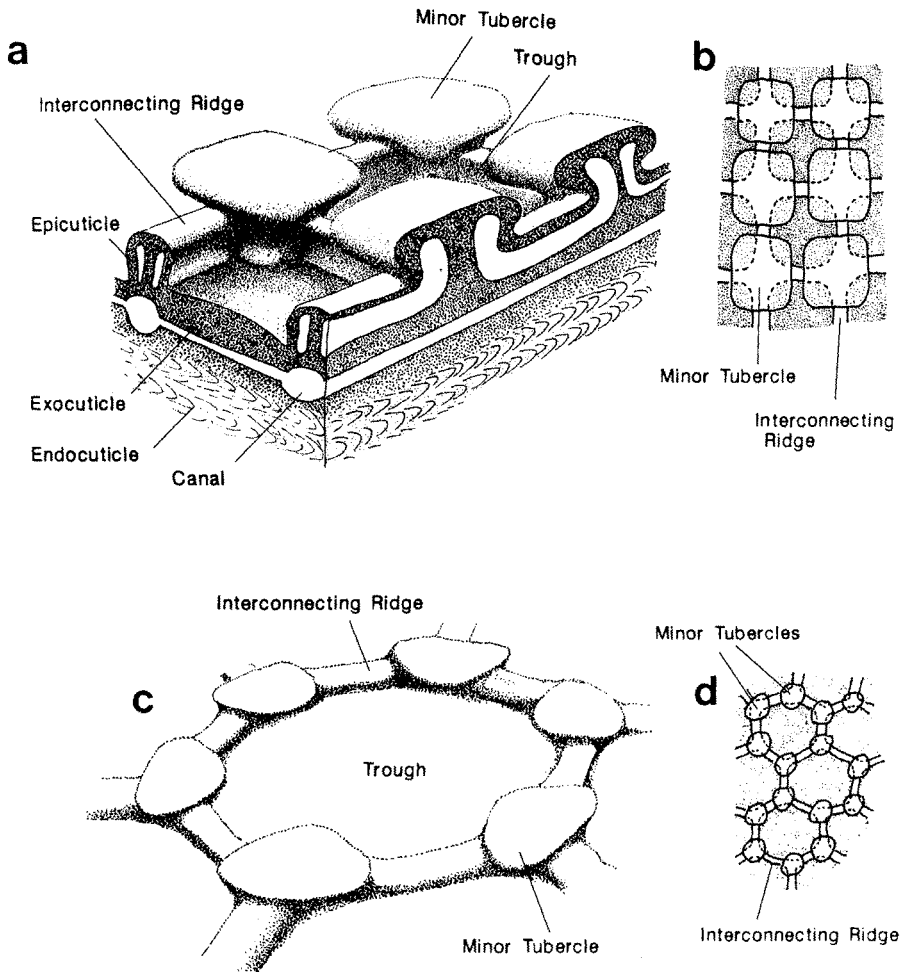


Fig. 4.9. Schematic diagrams of the surface structure of the cuticle of (a,b) *Anurida maritima* (Neanuridae) and (c,d) *Anuridella marina* (Neanuridae). When the animals are submerged, a layer of air is retained in the troughs between the minor tubercles (microtubercles) which functions as a plastron. Reproduced from King *et al.* (1990) by kind permission of the authors and Taylor and Francis.

1973; Hale 1969). However, while there are undoubtedly species-specific differences (Dallai 1972), care should be taken in reading too much into differences between taxa. The structure is due far more to selective pressures of the environment than to any underlying systematic influences (King *et al.* 1990; Leinaas 1980). The possibility of artefacts being introduced during preparation should not be overlooked.

The cuticle bears numerous small setae, sensory structures and larger spines of a wide variety of shapes. The spines may be long and thin, paddle-shaped, and are

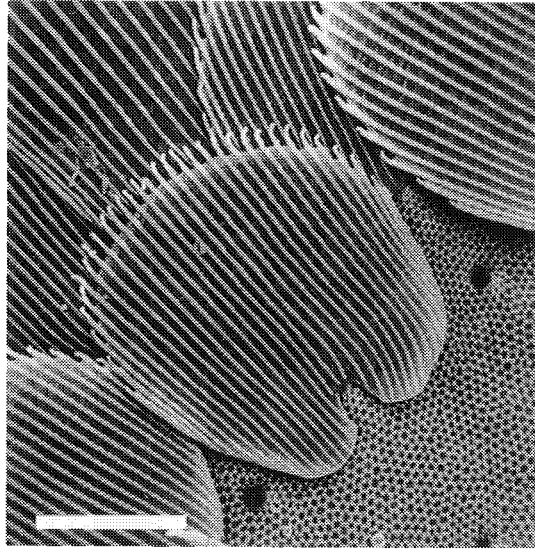


Fig. 4.10. Scanning electron micrograph of a cuticular scale of *Pogonognathellus flavescens* (Tomoceridae). Scale bar = 10 μm . Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

sometimes covered in numerous smaller spines giving them a 'plumose' appearance (Palacios-Vargas 1984). Some of the small spines have no apparent function but their positions on the segments have been used extensively in taxonomy, particularly for separating species, an approach known as 'chaetotaxy' (Section 5.2.4). Structures which are innervated are clearly functional and these are reviewed in Section 4.4. The classification of different types of setae and spines was reviewed extensively by Massoud and Ellis (1977). Some members of Entomobryoidea possess conspicuous scales which are easily detached from the cuticle (Fig. 4.10). In life, this gives many species a beautiful and characteristic iridescence.

Most surface-dwelling Collembola are pigmented, some very heavily (Noble-Nesbitt 1963c; Fig. 4.8). The dark violet species *Hypogastrura viatica* contains granules of an ommochrome pigment in the cells beneath the cuticle (Bouthier and Thibaud 1974). The level of pigmentation is correlated with latitude and altitude. The proportion of dark species increases as one nears the Poles or ascends high mountains (Rapoport 1969a). Heavily pigmented springtails warm up more quickly in the sun and can become active sooner than lighter coloured animals (Rapoport 1971). Pigmentation is obviously important for camouflage but it also protects surface-dwelling species from the damaging effects of ultraviolet light (Zinkler and Wilking 1989). Pollution may also influence colouration. The level of pigmentation of species of *Orchesella* and *Entomobrya* was greater near a source of industrial phosphate emissions than elsewhere in Germany (Fritzlär *et al.* 1986).

During moulting, springtails secrete an exuvial fluid which fills the space between the old and new cuticle (Barra 1969*a*; Krishnan 1969). This fluid may contain enzymes which dissolve the inner layer of the old cuticle (Noble-Nesbitt 1963*d*). Granular haemocytes have been observed within the fluid which may be involved in the separation of the old cuticle from the new (Barra 1970, 1977). *Folsomia candida* invariably eats its discarded exoskeleton after moulting and possesses symbiotic bacteria in its gut which are able to digest the chitin of the cuticle (Borkott and Insam 1990). Changes in the cuticular structure between moults are observed in species undergoing epitoky, cyclomorphosis and ecomorphosis (Cassagnau and Lauga-Reyrel 1987, 1992; Section 8.6).

4.2.4 *Pseudocelli*

Members of the Onychiuridae possess numerous circular structures on the head, thorax, abdomen and appendages which are known as 'pseudocelli' (Christian 1989*b*; Fjellberg 1973*b*; Hale 1969; Hale and Smith 1966; Pomorski 1993; Rusek 1984*a*; Weiner and Fjellberg 1994; Fig. 4.11). This is an unfortunate term since pseudocelli have nothing whatsoever to do with vision. All Onychiuridae are in fact blind. When irritated, these Collembola extrude fluid from glands beneath the pseudocelli.

The glands are composed of secretory cells which protrude into the body cavity and are in contact with the haemolymph (Rusek and Weyda 1981). The pseudocelli are made from epicuticle and are usually strengthened by ribs of thicker

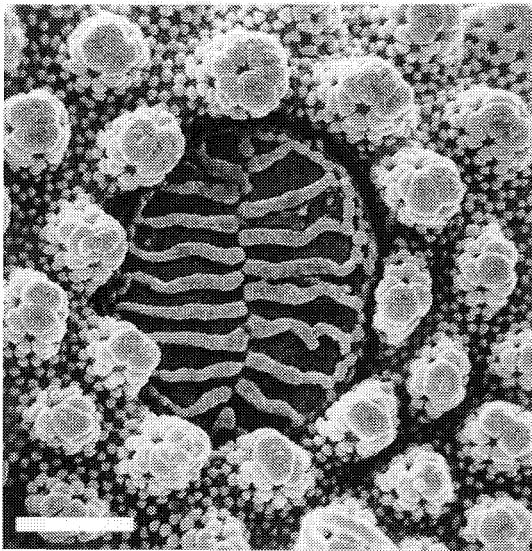


Fig. 4.11. Scanning electron micrograph of a pseudocellus of *Protaphorura* sp. (Onychiuridae). Defensive fluid is extruded from these pores when the animal is irritated. The number and position of pseudocelli has been used extensively in onychiurid taxonomy (cf. Fig. 5.13). Scale bar = 3 μ m. Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

cuticle (Fig. 4.11). Live specimens of *Protaphorura 'lata'*, can be induced to secrete defensive fluid by prodding with a needle. This needle then becomes 'active' and will repel other Collembola and potential predators if brought near to them (Usher and Balogun 1966). Onychiurid Collembola preserved in 70% alcohol are often covered in tiny brown spheres of defensive fluid that has solidified after secretion from the pseudocelli.

The number and distribution of pseudocelli has been used extensively by taxonomists for separating different 'species' of onychiurids (Gisin 1960a; Pomorski 1986, 1990c, 1993; Pomorski and Skarzynski 1989). The problems associated with this approach are discussed in Section 5.4.

4.3 Internal anatomy

4.3.1 Introduction

The smallest springtails such as *Mackenziella psocoides* (which is 250 μm in length; Fig. 3.14) are only a few times larger than a human liver cell. Nevertheless, even Collembola of this tiny size possess a full complement of internal organs. The basic arrangement in all springtails is a head containing salivary glands (Section 4.3.2) and labial nephridia or kidneys (Section 4.3.3; Fig. 4.12), and a digestive tract (Section 4.3.4; Fig. 4.14) which is surrounded by the other thoracic and abdominal organs. There is also a neurosecretory system and a brain (Fig. 4.18) formed from the anterior part of the ventral nerve cord (Chaudonneret 1987; Section 4.3.5; Fig. 4.17).

The body cavity contains a fat body where lipid and some waste products of metabolism are stored. In the Antarctic species *Cryptopygus antarcticus* (Frontispiece), more than 25% of the body weight is lipid at certain times of the year, most of which is stored in the fat body (Convey 1992). The fat content tends to be higher in cave species than in surface-dwelling Collembola (Thibaud and Vannier 1978; Vannier and Thibaud 1984).

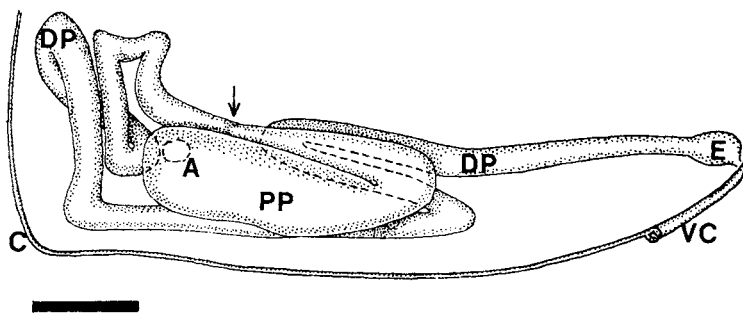


Fig. 4.12. Semi-schematic diagram of a labial nephridium of *Orchesella cincta* (Entomobryidae). A, aperture showing connection with sacculus (not shown); C, cuticle; DP, distal part; E, end sac; PP, proximal part; VC, ventral channel or groove; arrow, transition of PP to DP. Scale bar = 10 μm . Reproduced from Verhoef *et al.* (1979) by kind permission of the authors and Springer-Verlag.

There is a complicated system of internal muscles (Bretfeld 1963; Eisenbeis 1978; Maki 1938; Manton 1977). In extremely flattened species such as *Nepalimeria dal* from central Nepal, the muscular pillars between the internal surface of the dorsal and ventral body walls are increased in number to facilitate better grip on the substrate (Cassagnau 1993a). Circulation of the blood which bathes the organs is maintained by the dorsal blood vessel or 'heart'. Unlike most other insects, Collembola appear to lack specialised circulatory organs for pumping blood into the antennae (Pass 1991). The blood of *Tetradontophora bielanensis* contains at least five different types of haemocytes (Klag and Ksiazkiewicz-Kapralaska 1990; Ksiazkiewicz-Ilijewa and Rosciszewska 1979). Females and males possess well-developed ovaries or testes which undergo changes in morphology related to cycles of sexual activity, and in some cases, season (Lauga-Reyrel 1977, 1984d). The structure of the reproductive organs is described in Section 8.2.

Actaletidae and some Sminthurinae are the only springtails with tracheae. In *Sminthurus viridis* for example, these form a branching system of tubes which open to the air *via* a pair of ventral spiracular openings between the head and thorax (Davies 1927; Section 6.4). Tracheae probably evolved independently after Collembola branched off from the stem leading to other insects (Xué *et al.* 1994). Members of the Spinothecinae have unusual 'neck organs' which may be involved in gaseous exchange (Greenslade 1982b).

4.3.2 Salivary glands

Collembola have three or four pairs of salivary glands which secrete enzymes onto the food in the buccal cavity. In those springtails which have piercing rather than grinding mouthparts, salivary fluid may be extruded onto the food to form a liquid suspension which is then drawn back into the mouth. Some neanurids have very large salivary glands which extend posteriorly into the prothorax (Lee 1980b). For example, *Rambutanura yoshii* from Thailand is only 5 mm in length but four lobes of its salivary glands are each more than 0.5 mm across and contain more than 100 cells (Deharveng 1988b). The nuclei of these cells contain polytenic (giant) chromosomes which facilitate more rapid transcription of the genes coding for the synthesis of salivary enzymes (Cassagnau 1968a; Lee 1981, 1985a). The structure of these chromosomes has been used for taxonomic purposes (Section 5.2; Figs. 5.5, 5.6).

4.3.3 Labial nephridia

A pair of labial nephridia are situated in the caudoventral part of the head (see Fig. 4.12). Each is composed of a sacculus in which podocytes are present, and a tubule consisting of a proximal part and a distal part. The distal parts of both nephridial tubules meet in an end-sac posterior to the labium (Verhoef *et al.* 1979). The fluid which collects in the sac is usually hypoosmotic to the haemolymph and can be regarded as urine (Verhoef *et al.* 1983). Urine is discharged into the ventral groove (Fig. 4.13) and passes to the ventral tube by capillary action (Verhoef *et al.*

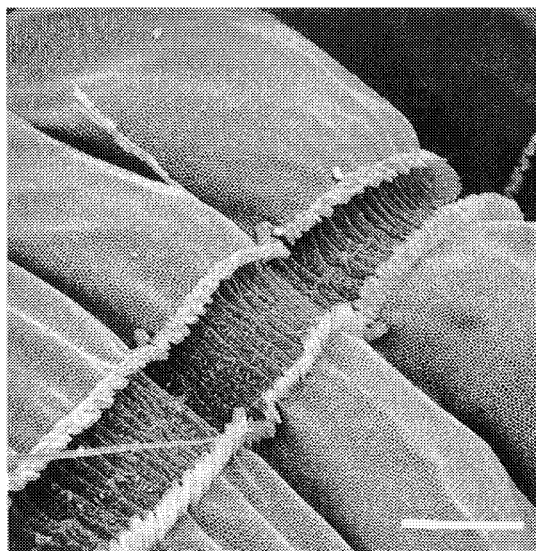


Fig. 4.13. Scanning electron micrograph of the ventral groove which runs between the mouth region and the ventral tube of *Pogonognathellus flavescens* (Tomoceridae) on the ventral side of the thorax. Scale bar = 20 μ m. Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

1983). The epithelium of the nephridial tube has the ultrastructural characteristics of resorbing cells so the nephridia almost certainly perform the functions of 'ultrafiltration-reabsorption' kidneys (see Section 6.3.2). Thus the labial nephridia, together with the ventral tube, are involved in ionic and water balance (Verhoef and Prast 1989).

Also present are a pair of rudimentary nephridial organs which appear to function in storage excretion as they have no efferent ducts (Humbert 1975).

4.3.4 Digestive tract

The digestive system of Collembola consists of a foregut, an enlarged sac-like midgut, and a small tubular hindgut (Figs. 4.14, 4.15). The foregut and hindgut are formed from invaginations of embryonic ectoderm and are lined with cuticle which is shed at every moult. The midgut is endodermal in origin with microvilli in direct contact with a peritrophic membrane that is secreted by a ring of cells posterior to the junction between the foregut and midgut. There are no large diverticulae or midgut glands that arise from the alimentary tract. Malpighian tubules are absent although there are tiny 'malpighian papillae' at the anterior end of the hindgut (Dallai 1980c). The midgut is surrounded by a network of circular and longitudinal muscles which mix food in the lumen and force residues of digestion into the hindgut by contraction (Dallai *et al.* 1989). The fat bodies which lie in the haemolymph are in close contact with the basal surface of the midgut from which they presumably absorb products of digestion that pass across the basement lamina.

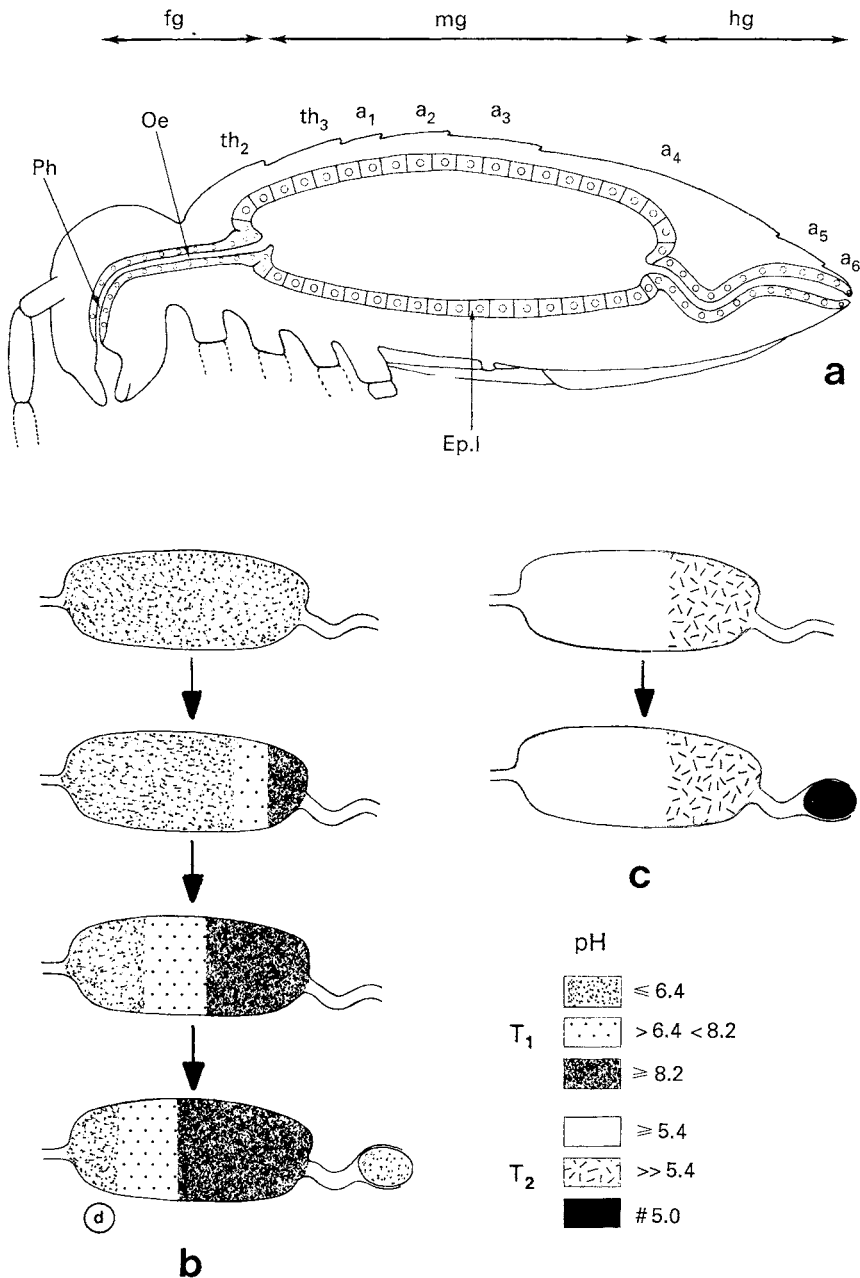


Fig. 4.14. Schematic diagrams of the digestive system of *Sinella coeca* (Entomobryidae). (a) Section through the midline. Ep.I., intestinal epithelium; fg, foregut; hg, hindgut; mg, midgut; oe, oesophagus; Ph, pharynx. (b) Changes in pH during the passage of food through the lumen of the gut revealed by staining with Phenol Red (T₁) (c) pH of the gut contents of the last two stages of digestion (T₂) shown in (b) revealed by staining with Bromocresol Green. Reproduced from Humbert (1974b) by kind permission of the author and Editions Gauthier-Villars.

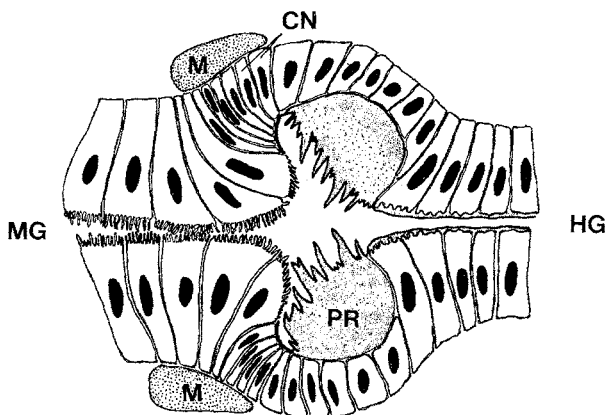


Fig. 4.15. Schematic diagram of the 'pyloric region' of Collembola at the junction of the midgut and hindgut. CN, connecting cells; HG, hindgut; MG, midgut; M, muscle; PR, pyloric ring cells. Reproduced from Dallai (1980c) by kind permission of the author and Accademia dei Fisiocritici, Siena.

The midgut epithelium consists of a single layer of columnar or cuboidal cells which contain organelles typical of insect digestive cells. These include a single nucleus, rough endoplasmic reticulum, mitochondria and Golgi bodies (Humbert 1979b; Klag *et al.* 1981; Krysztofowicz *et al.* 1973; Fig. 4.16). The cells secrete enzymes (Ferard and Poinso-Balaguer 1989) and absorb products of digestion from the lumen (Eisenbeis and Meyer 1986). The pH of the lumen is optimised for the activity of different enzymes and is slightly acidic (approximately pH 6) in the anterior part of the midgut and hindgut, and alkaline (approximately pH 8) in the posterior midgut (Humbert 1974b; Fig. 4.14).

Pogonognathellus flavescens (Tomoceridae) is apparently able to secrete cellulase. Zinkler *et al.* (1987) showed that 18% of ^{14}C -labelled cellulose was assimilated during a single transit of the gut by this species. The assimilation rate was essentially unchanged in springtails fed with antibiotics supporting an endogenous origin of cellulases rather than a microbial source.

Some Isotomidae possess a dense 'terminal web' of proteinaceous microfilaments of 7 to 10 nm in diameter just below the microvilli of the midgut cells (Barra and Poinso-Balaguer 1987; Dallai 1994b; Dallai *et al.* 1993; Fig. 4.16). This is perforated with holes of 100–140 nm in diameter. The exact function of the terminal web is not known although it may give some degree of structural integrity to the apical region of the midgut epithelium in addition to the support provided by the intercellular junctions (Dallai 1975a).

The alimentary canal between the midgut and hindgut bears a muscular sphincter and is known as the *pyloric region* (Fig. 4.15; Dallai 1980c). It consists of three zones:

- the *posterior midgut cells* characterised by a decreased number of cellular organelles and inclusions (Poinso-Balaguer and Barra 1977)

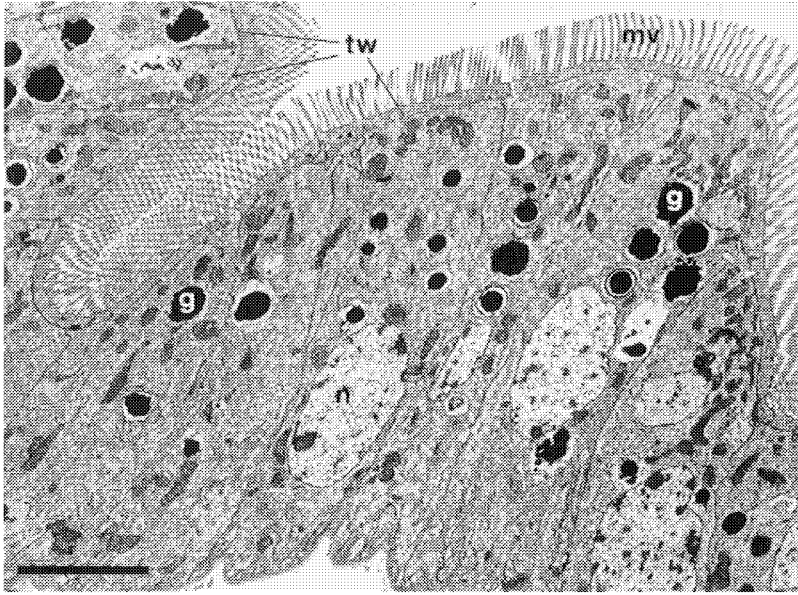


Fig. 4.16. Transmission electron micrograph of a section through the midgut of *Isotoma palliceps* (Isotomidae). The cells contain numerous calcium phosphate excretory granules (g) which are lost in the faeces when the midgut cells are voided during moulting. mv, microvilli; n, nucleus; tw, terminal web. Reproduced from Eisenbeis and Meyer (1986) by kind permission of the authors and the University of Siena.

- the *connecting cells* lined with thin cuticle with bundles of longitudinal microtubules that enable them to resist the strong tension of the pyloric region
- the *pyloric ring cells* with a very thick cuticle bearing apical denticulations (Dallai and Callaini 1979).

Faecal pellets are formed in the rectum where water is absorbed into the hindgut cells across the thin cuticular lining (Verhoef *et al.* 1979).

Bacteria and fungi are often observed in the lumen of the gut (Christian 1993b). Many of these are ingested with the food and are important components of the diet. Others may form resident symbiotic populations which secrete enzymes which the springtails are unable to manufacture for themselves (Borkott and Insam 1990; Urbášek and Rusek 1994). Some fungal spores are resistant to digestion and remain viable after passage through the alimentary tract (Vannier 1979b).

One unusual feature of the midgut is the presence of large amounts of waste material which build up in the cells during intermoult (see Fig. 4.16). The excretory vacuoles contain uric acid, and concentrically structured granules of calcium phosphate which may also contain non-essential metals such as lead, and essential metals such as zinc and iron which are surplus to requirements (Humbert 1974a, 1977; Van Straalen *et al.* 1987). These granules are found in the midgut epithelial cells of most invertebrates (Hopkin 1989, 1990; Hopkin *et al.* 1989).

Towards the end of an intermoult period, the permeability of the midgut cells increases and they begin to degenerate (Humbert 1978a). The whole midgut is sloughed off into the lumen just before ecdysis and a new one is formed from small regenerative cells which lie on the basement lamina (Humbert 1979b; Hutasse 1982). Thus soon after a moult, a faecal pellet is voided which contains waste products accumulated by the midgut during the previous instar (Thibaud 1976b). Regular replacement of the midgut may be 'expensive' in terms of resources, but it is a very effective way of ridding the body of toxins (Humbert 1978b, 1979a; Van Straalen *et al.* 1987).

During ecomorphosis (Section 8.6), the midgut appears to go into a 'dormant' stage where digestive activity is reduced but accumulation of excretory products, including calcium phosphate granules, is greatly increased (Bannon and Engstrom 1980; Lauga-Reyrel 1980).

4.3.5 *Nervous and neurosecretory systems*

The nervous system comprises a 'brain' of supra- and suboesophageal ganglia (Tyszkiewicz 1981) and three ventral thoracic ganglia. The abdominal ganglia are fused to the metathoracic ganglion which usually extends into the first abdominal segment (Brauner 1981; Fig. 4.17).

The neurosecretory system is similar to that of other insects and is involved in the secretion of hormones (Cassagnau 1971a; Cassagnau and Juberthie 1966, 1967a,b; Cassagnau *et al.* 1968; Lauga-Reyrel 1984a,b; Fig. 4.18). For a detailed review of the structure of the neurosecretory system, and a discussion of its evolution, see Juberthie and Cassagnau (1971).

4.4 **Sense organs**

4.4.1 *Introduction*

There are two main approaches to studying the sensory systems of terrestrial invertebrates. The first is to expose animals to certain stimuli and to examine their responses. The second to examine the ultrastructure of the sense organs and to try and interpret their function from the types of cells present. In large animals, it may be possible to directly record impulses from nerves that innervate sensory cells and to gain direct evidence of the involvement of particular organs in detecting stimuli. However, Collembola are so small that such direct evidence is extremely difficult to obtain. Most researchers on springtails have therefore concentrated on interpreting function from structure, or have monitored the behaviour of whole animals under specific conditions.

Collembola have been shown to respond to taste, smell, light, touch and sound vibration, although particular species have lost one or more of these senses during their evolution (e.g. some soil and cave species are blind). For example, *Protaphorura armata* and other species are attracted to volatile compounds

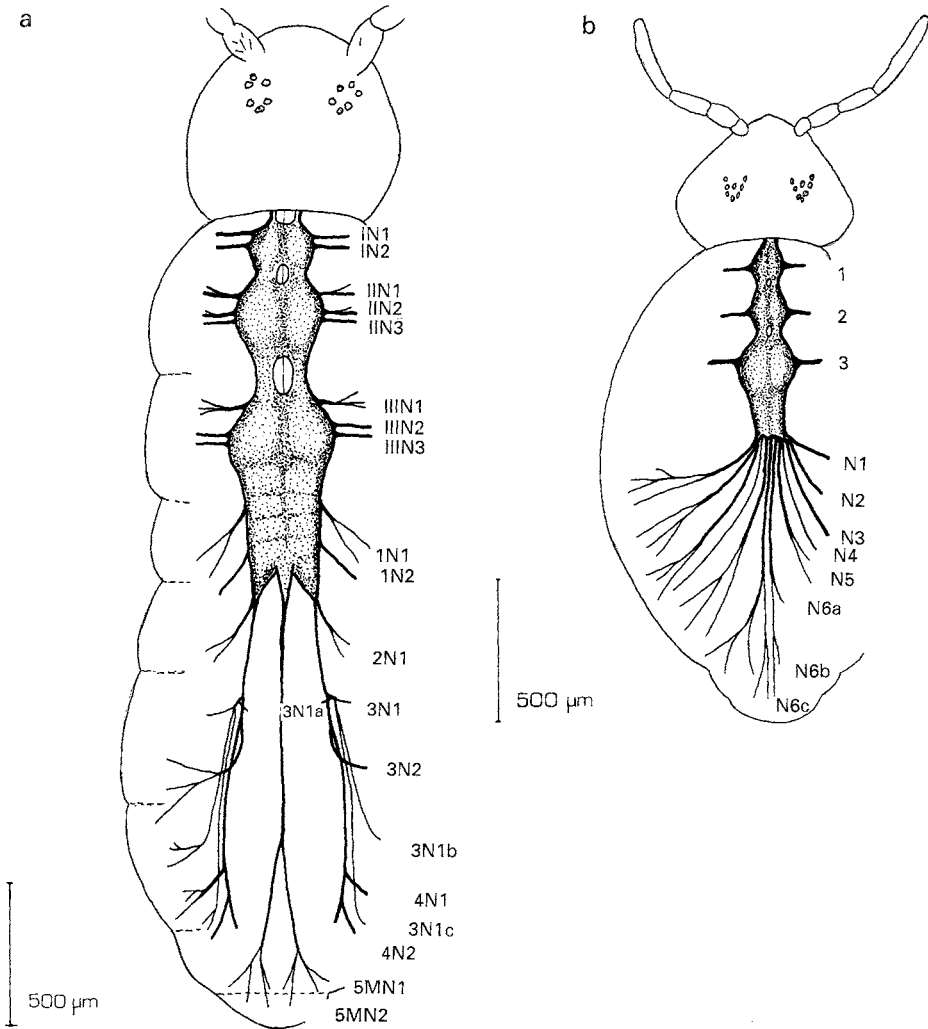


Fig. 4.17. Thoracic and abdominal nervous systems of (a) *Isotoma viridis* (Isotomidae) and (b) *Allacma fusca* (Sminthuridae). Reproduced from Brauner (1981) by kind permission of the author and Gustav Fischer.

extracted from their preferred fungal food sources (Bengtsson *et al.* 1991; Hedlund *et al.* 1995). *Folsomia fimetarioides* and *Isotomiella minor* avoid soils polluted with zinc and copper because they can presumably ‘taste’ the high levels of metals (Bengtsson *et al.* 1994a). Springtails may also respond to changes in atmospheric pressure (Meier *et al.* 1988; Zettel 1984a), humidity, temperature, and concentration gradients of oxygen and carbon dioxide (see Chapter 6).

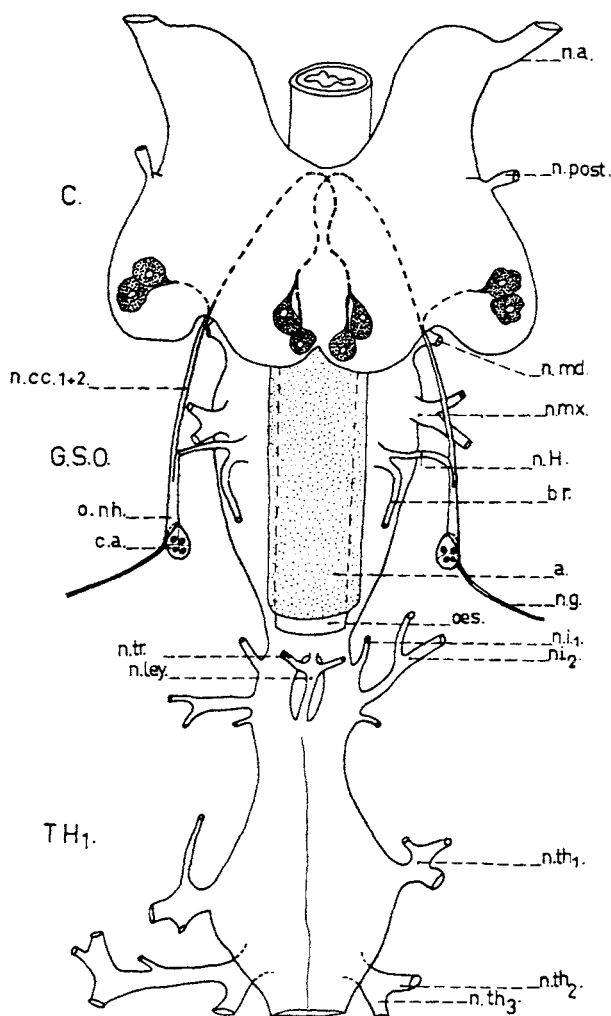


Fig. 4.18. 'Brain' and neurosecretory system of *Kalaphorura tuberculata* (Onychiuridae). br., recurrent branch of nerve of Hoffmann; a, aorta; C, brain; c.a., corpus allatum; G.S.O., suboesophageal ganglion; n.a., antennal nerve; n.cc.1+2, corpus cardiacum nerves 1 and 2; n.g., mandibular branch of nerve of Hoffmann; n.H., nerve of Hoffmann; n.i.₁, n.i.₂, first and second intercalary nerves; n.ley., nerve of Leydig; n.md., mandibular nerve; n.mx., maxillary nerve; n.post., postantennal nerve; n.th.₁, n.th.₂, n.th.₃, first, second and third prothoracic nerves; n.tr., transverse nerve; oes, oesophagus; o. nh., neurohaemal organ; TH₁, prothoracic ganglion. Reproduced from Cassagnau and Juberthie (1967a) by kind permission of the authors and Société d'Histoire Naturelle de Toulouse.

The basic structure of insect sense organs has been reviewed extensively on numerous occasions and will not be described in detail here (see for example Altner and Prillinger 1980; Gullan and Cranston 1994). The following account therefore concentrates on structures which are peculiar to, or which are particularly well developed in, Collembola.

4.4.2 Sensory structures on the antennae

The antennae are richly endowed with sensory structures, particularly at the tip (Slifer and Sekhon 1978; Fig. 5.9). The antennae are often waved in the air to pick up airborne chemicals as the animal walks along, and tapped against the ground to pick up stimuli from the substrate. The antennal segments bear normal setae, which detect air currents and vibrations, and parallel-sided, thin-walled chemosensory setae (sensilla). Where sensilla exist in close association they may form a sensory complex. All Collembola (except Gulgastrurinae, see Lee and Thibaud 1987) possess such a sensory complex on the third antennal segment which consists of two or more sensilla protected by guard setae (Gough 1973*b*; Snider 1969*a*; Fig. 4.19). These sensilla are covered in pores of 5 nm in diameter (Altner and Thies 1972). Other sensory structures for which functions have yet to be ascribed include those on the base and first antennal segment of Entomobryoidea (Hüther 1986).

The tip of the antenna of Collembola bears a complex of sensory 'hairs' and receptors (Massoud and Delamare-Deboutteville 1969). This complex may be highly developed in species which live in caves and which have reduced sensory structures on other parts of the body (Lee and Thibaud 1987). Most species also possess an eversible sac on the end of the antenna containing sensory and gland cells which are innervated by neurosecretion (Altner and Kuhn 1989; Altner and Thies 1978; Slifer and Sekhon 1978). In *Hypogastrura socialis*, the sac may be involved in pheromone production (Altner and Thies 1973). The antennal complex of this species bears two terminal-pore sensilla which contain cells receptive to chemical and mechanical stimuli (Altner and Altner 1985; Altner and Ernst 1974).

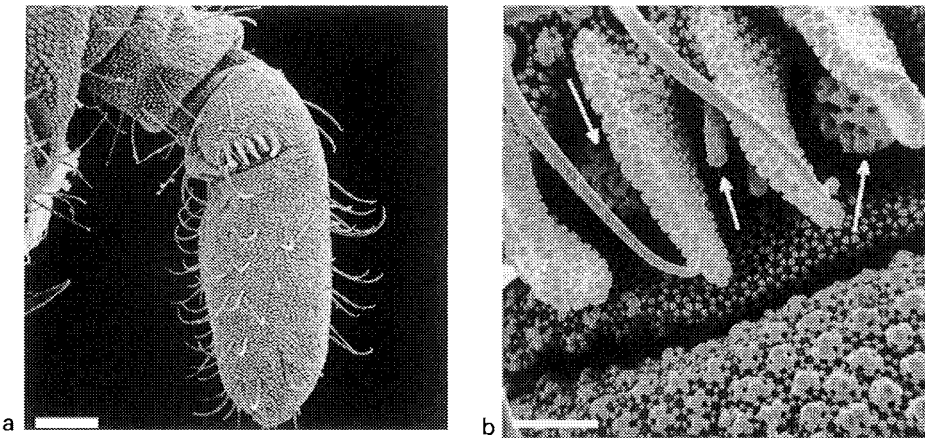


Fig. 4.19. Scanning electron micrographs of the antenna of *Protaphorura* sp. (Onychiuridae). (a) Distal part of antenna showing sensory complex on section 3. Scale bar = 25 μm . (b) Close-up view of sensory complex showing the comb-like subdivisions and modified sensilla (arrows). Scale bar = 3 μm . Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

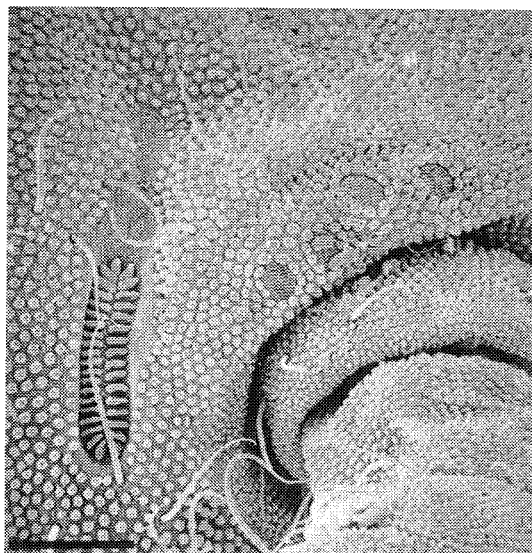


Fig. 4.20. Scanning electron micrograph of the region at the base of the antenna of *Protaphorura* sp. (Onychiuridae). The long ribbed structure on the left is the post antennal organ. The four small oval structures are pseudocelli (cf. Fig. 4.11). Scale bar = 25 μ m. Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

The position of the antenna is monitored by proprioceptors (scolopidia, see Paulus 1974) associated with the cuticle (Altner and Thies 1984), and levator and depressor muscles (Altner 1988).

4.4.3 Postantennal organ

Many species of Collembola possess a postantennal organ (PAO) posterior to the base of each antenna (Altner *et al.* 1971; Dallai 1971a; Dallai and Sabatini 1981). The PAO appears to be absent in some families such as Entomobryidae, and in Sminthuridae it takes the form of a 'peg' (Altner *et al.* 1970). In Tomoceridae, the PAO may be present only in the juvenile stages, although this is not the case for every species in the family (Ireson and Greenslade 1990). The structure of the PAO has long been of taxonomic importance, especially in Onychiuridae (Handschin 1921; Figs. 4.20, 5.12).

In *Hypogastrura socialis*, the PAO is typically in the form of a four lobed protuberance located in a shallow pit. In *Anurida maritima*, there are 6–9 of these lobes (Fjellberg 1980a). In Onychiuridae, the organ consists of an elongated rosette of up to 30 or more smooth or lobed protuberances set in an elongated furrow (Hale 1969; Handschin 1921; Fig. 4.20). In Isotomidae, the PAO is an oval or horn-shaped cuticular plate elevated above the surrounding cuticular surface (Altner and Thies 1976). In spite of the diversity of external appearance, there are similarities in the internal structure of the PAO across families. Most PAOs have a system

of pores 5–10 nm in diameter, a single sensory cell with two branching ciliary outer segments, reduction of the outer receptor lymph cavity and a coating of dense material around the dendrites (Altner and Thies 1976; Karuhize 1971). The function of the PAO is not completely understood and it may be sensitive to smell, humidity or temperature (Altner and Thies 1976).

4.4.4 Eyes

Springtails normally have a maximum of eight ocelli on each side of the head (Fig. 4.21), although very occasionally an extra ‘aberrant’ ocellus may be present (Christian and Schaller 1982; Mitra 1972). Epedaphic species infrequently show a reduction in this number but cave and euedaphic Collembola often have reduced eyes and are frequently blind (Barra 1973; Thibaud 1976*a*; Section 9.6). The ocelli are formed from fused ommatidia (Barra 1971*a,b*; Paulus 1971, 1972). In *Bonetogastrura cavicola*, some specimens may show a reduction in the number of ocelli from the normal 8 + 8 plan to as few as 2 + 2; some individuals even have a different number of ocelli on opposite sides of the head (Thibaud-Brauner 1985). The structure of the ommatidia is very similar to those of Crustacea lending support to the sister group status of Insecta/Crustacea.

During migration across snow, *Hypogastrura socialis* uses its eyes to calculate the angle of the sun before making a jump and may be able to detect the angle of polarisation of light (Hågvar 1995; Figs. 9.1, 9.2).

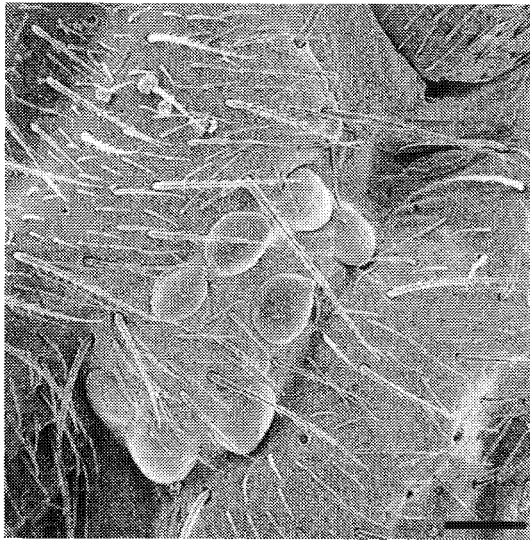


Fig. 4.21. Scanning electron micrograph of the eye of *Isotomurus palliceps* (Isotomidae) with eight well-developed ommatidia. Scale bar = 25 μ m. Reproduced from Eisenbeis and Wichard (1987) by kind permission of the authors and Springer-Verlag.

4.4.5 Other sensory structures

Anyone who has viewed the surface of Collembola in a scanning electron microscope will be aware of the profusion of setae and sensory 'hairs' which cover the body and the appendages. Long setae in sockets, such as trichobothria (Betsch and Waller 1989), detect air currents and vibrations whereas shorter, parallel-sided setae are probably chemosensory (Massoud and Ellis 1977). Some setae may perform more than one function, for example the long tibiotarsal spatula 'hairs' in *Pogonognathellus flavescens* which combine mechanosensitivity with secretion of an adhesive substance (Blottner and Eisenbeis 1984).

The different types of setae have been classified by André (1988*b*) who made a comprehensive study of *Xenylla jocquei* on which he found a total of 1010 'setiform organs' on the surface of the body and appendages. André (1988*a*) called this comprehensive approach 'phanerotaxy' and has stressed the importance of completeness when using the presence or absence of particular setae in taxonomy (see Section 5.2.3).

Information on stresses in the exoskeleton is provided by *oval organs* embedded in the cuticle (Snider and Loring 1984). Internal and external *proprioceptors* 'monitor' the positions of appendages (Altner and Thies 1984; Crouau *et al.* 1987).

4.5 Structure and function of the 'spring'

The springing organ or *furca* is the most characteristic feature of Collembola. The furca is well developed in the majority of surface-dwelling springtails although in some euedaphic species which live all their lives in the soil, it is greatly reduced, or even absent altogether. Species with a large furca tend to make single, but long jumps, to escape from predators whereas those in which the furca is reduced make frequent short jumps to cover the same distance (Bauer and Christian 1987).

The evolutionary origin of the furca is from a pair of appendages on the fourth abdominal segment (see Fig. 4.1). These fused basally to form the *manubrium* (Eisenbeis and Ulmer 1978). The two distal parts remained separate and developed into the paired *dens*. Each part of the dens bears a modified claw or *mucro* at its tip which is often 'toothed' and which may vary in shape between moults within species, or even the same individual (Goto and Ögel 1961). The mucro provides the friction with the substrate, the teeth helping to reduce slipping on the ground (Leinaas 1981*c*). The mucro of Collembola which live on water is often expanded into a tiny paddle which prevents it from breaking through the surface tension during a jump. The arrangement of setae on the furca, shape, and number of teeth on the mucro, are extremely important for taxonomy (Eisenbeis and Meyer 1986). The furca was an ancient development and was present at least 400 million years ago (Greenslade 1988).

The furca is most strongly developed in epedaphic Collembola which use their considerable jumping ability for rapid locomotion and to escape from predators (Christian and Völlenkle 1979). *Entomobrya dorsalis* is only 2 mm in length, but

can jump for a distance of more than 16 cm (Bauer and Christian 1986). *Sminthurus viridis* takes off with a velocity of 1.4 m s^{-1} with an acceleration of 970 m s^{-2} (Christian 1979). Most springtails become airborne within 50 ms of the start of a jump. The fastest is *Allacma fusca* which takes only 12 ms (Bauer 1990). There are several species of ants (Hölldobler and Wilson 1990) and ground beetles (Bauer 1982b) which have evolved highly specialised feeding apparatus for catching springtails (see Fig. 7.6). The 'evolutionary race' has been won to some extent by predators which can trap springtails more rapidly than they can escape. The carabid beetle *Loricera pilicornis* closes an array of specialised trap setae on its antennae within 12 ms, whereas it takes 26 ms for the furca of its prey *Heteromurus nitidus* to push it off the ground (Bauer 1982a; Bauer and Völlenkne 1976). However, *Sminthurus viridis* generates enough kinetic energy during take off to bend the setae which is sufficient to open the trap and allow the springtail to escape (Hintzpeter and Bauer 1986).

The furca is normally held in place by a 'catch' or *tenaculum* (sometimes called the *retinaculum*) on the ventral side of the third abdominal segment. However, this structure does not seem to be essential for leaping in some springtails which

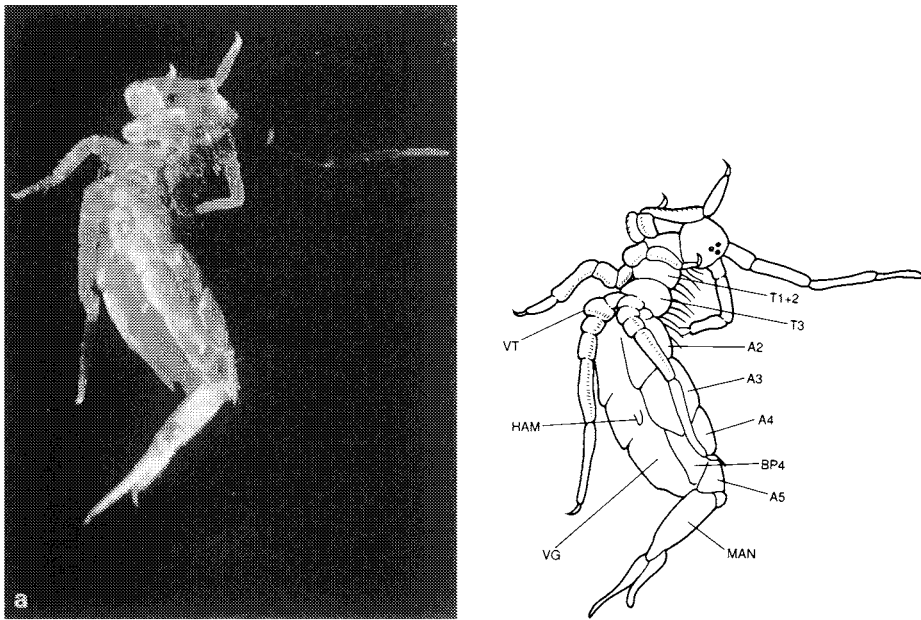


Fig. 4.22. High speed flash photograph (a) and diagrammatic interpretation (b) of *Orchesella villosa* (Entomobryidae) of 6 mm in length in mid leap. Note the pronounced dorsiflexion of the body between the thorax and abdomen. A2–5, abdominal segments 2–5; BP4, basal plate of fourth abdominal segment; HAM, hamula (= tenaculum); MAN, manubrium; T1+2, T3, thoracic segments; VG, ventral groove of abdomen (not to be confused with thoracic ventral groove); VT, ventral tube. Reproduced from Brackenbury and Hunt (1993) by kind permission of the authors and the Zoological Society of London.

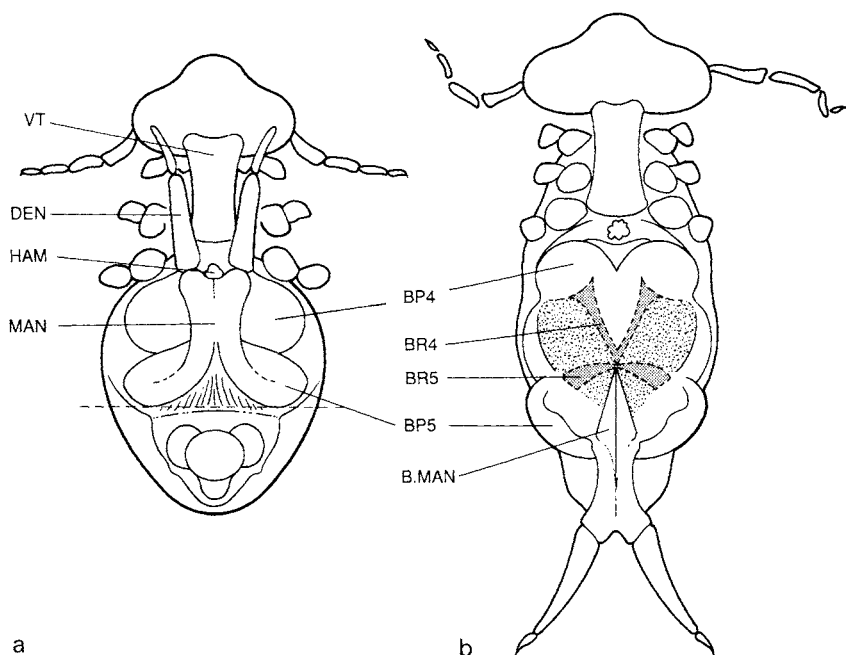


Fig. 4.23. Ventral view of *Dicyrtomina ornata* (Sminthuridae, cf. Fig. 3.15) of 1.5 mm in length with furca folded (a) and extended (b). B.MAN, manubrial base; BP4, BP5, basal plates of abdominal segments 4 and 5; BR4, BR5, basal rods of abdominal segments 4 and 5; DEN, dens; HAM, hamula (= tenaculum); MAN, manubrium; VT, ventral tube. Reproduced from Brackenbury and Hunt (1993) by kind permission of the authors and the Zoological Society of London.

jump just as well with the tenaculum removed as an uninjured animal (Christian 1978).

The jump is achieved by rapid flexion of the furca away from the body. *Pogonognathellus longicornis* and *Dicyrtomina ornata* have a click mechanism involving contraction of internal muscles and deformation of the abdominal sclerites (Figs. 4.22, 4.23). Eversion of the springing organ involves a hydroelastic mechanism based on haemocoel pressurisation and increased tension in the abdominal sclerites provided by muscles (Brackenbury and Hunt 1993). The muscles involved in performing the jump are specialised for bursts of anaerobic activity (Tosi and Ferrari 1989; Zinkler and Schroff 1989). After a series of jumps, there is a significant decrease of ATP while levels of ADP and AMP increase (Ruhfus and Zinkler 1995). The muscles soon become fatigued if the springtail is forced to make several jumps in rapid succession.

During a jump, a collembolan may turn through several somersaults. The orientation during landing is unpredictable but they soon right themselves. For a discussion of the selective pressures involved during the evolution of jumping in all animals, see Alexander (1995).

Taxonomic methods and the species concept in Collembola

5.1 Introduction

The great majority of genera listed in Appendix A are well characterised. Most discussions about genera among taxonomists concern which species to place in them, rather than their validity. Providing the boundaries of genera are well defined, and can be shown convincingly by cladistic analysis to be monophyletic units, I see no good reason why existing genera should not be split into two or more genera, or why subgenera should not be raised to generic rank. Although some authors still use the category of subgenus in their publications (e.g. Fjellberg 1991*b*; Snider 1990*a,b*), it might be preferable to abandon subgenera altogether as their use frequently causes confusion.

The majority (and often the most vociferous!) of arguments between taxonomists concern the boundaries of species. Disagreements occur between the so-called 'lumpers' and 'splitters'. Lumpers favour broad definitions of species and consider that a new species should not be erected unless the individual animals within it are very distinct from any previously described species. Splitters tend to award new species status on the basis of very minor differences between individuals, sometimes describing a new species from a single damaged specimen. My own view is that taxonomists should be conservative since excessive splitting, without the evidence to back it up, gives a false view of the extent of biodiversity.

Understanding the species concept is vital for studies on biodiversity (Harper and Hawksworth 1994), conservation (Vane-Wright *et al.* 1991), ecology (Behan-Pelletier 1993; Petersen 1995) and ecotoxicology (Hågvar 1994; Hopkin 1993*a*, in press; Van Straalen 1993*b*). Biodiversity is often determined by simply counting the number of species at a particular location. Even the more complicated estimates of biodiversity still rely on comprehensive species lists (Usher 1983). It is obvious that estimates of biodiversity depend fundamentally on the accuracy of such lists, and that these estimates will differ wildly if a checklist for one country has been prepared by a lumper, and for another by a splitter (Hammond 1994). Estimates of the number of described and undescribed species in the world depend so much on differences of opinion on the boundaries of species that it is surprising that this factor is so rarely taken into account.

In his excellent and thought-provoking book on systematics, Minelli (1993) stated that 'in systematic biology, no concept has been the subject of such heated debate as the species concept'. This is certainly the case for Collembola and in this

Chapter I will attempt to explain why there has been, and continues to be, so much disagreement over a question which ought to have a simple answer. How many species of springtails are there?

5.2 Methods of defining species

5.2.1 Species concepts

Many books and papers have been written on the species concept. Excellent discussions of the issues involved can be found in Heywood (1995), Minelli (1993), O'Hara (1994), Rand and Wilson (1993), Whittemore (1993), Wilson (1992) and World Conservation Monitoring Centre (1992). The most extreme view is that 'species are individual organisms' but this approach has, not surprisingly, received little support.

The general consensus among evolutionary biologists is that new species arise through diminished gene flow between different groups of individuals of an existing species. These groups become separated, either geographically, or locally into different niches, then evolve along unique lines in response to differing selective pressures (Rice and Hostert 1993; Wilson 1992). Species boundaries are usually clear-cut but in small insects such as Collembola, this is not always the case. The most widespread definition, the *biological species concept*, was developed in the 1930s and 1940s. This concept states that '*species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups*' (Mayr, 1940). More simply, '*a species is a population whose members are able to interbreed freely under natural conditions*' (Wilson 1992). For practical reasons, these definitions are good working assumptions, despite a few drawbacks (Heywood 1995; Minelli, 1993; O'Hara, 1994).

However, outside large, well-studied groups such as birds and mammals, it is rare for the taxonomist to test for reproductive isolation in their species. In many cases this is impossible as most work is conducted on dead specimens. In relatively poorly studied groups such as Collembola, many species should be considered as 'morphospecies' (Cassagnau 1977; Christiansen and Culver 1968, 1969). Within genera, the degree of difference between two groups of individuals that constitutes evidence of reproductive isolation is heavily dependent on the opinion of the taxonomist (Lawrence, 1979). As we shall see later, this situation may lead to large differences in the levels of perceived biodiversity within at least one Subfamily of Collembola due to human nature rather than nature! (Section 5.4).

Some taxonomists have used the concept of operational taxonomic units (OTUs) to describe a group of individuals which are morphologically similar, and which might or might not represent a single biological species. Four main types of OTUs can be recognised in Collembola (Fig. 5.1).

- *Type A* OTUs comprise groups of very similar biological or morphospecies. The category of species groups is useful for simple keys, or where there is controversy as to species boundaries, e.g. *Tullbergia krausbaueri* 'group' (Dunger 1986).

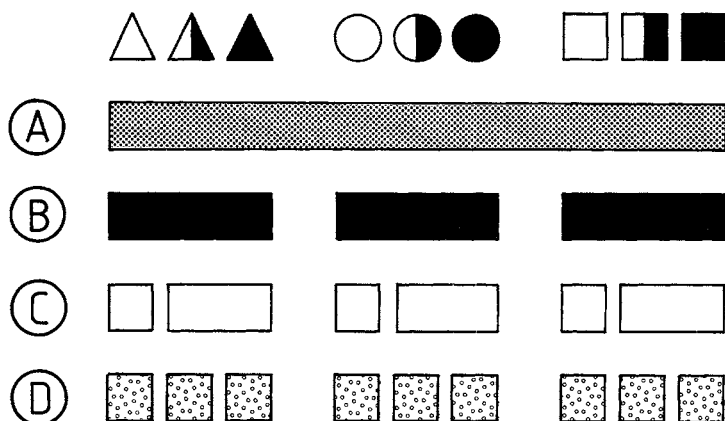


Fig. 5.1. Schematic diagram illustrating the concept of operational taxonomic units (OTUs) as applied to Collembola. Nine individuals are present in a collection comprising three biological species represented by triangles, circles and squares, each with one of three levels of pigmentation (top row). A 'lumper' would consider all nine individuals to represent a single species (row A). The boundaries of true biological species are shown in row B. A 'splitter' would regard unpigmented and pigmented specimens as separate species (row C) and an 'extreme splitter' would award species status to all nine varieties (row D). See text for further details.

- *Type B* OTUs are true biological species. All the individuals within a type B OTU can interbreed amongst themselves, but are reproductively isolated from other Collembola.
- *Type C* OTUs recognise constant varieties below the level of biological species. If the varieties have a genetic basis, it is legitimate to call them *subspecies* (Christiansen 1958b). However, if this is not the case then they should be referred to as *forms*. Within a species, individuals from separate subspecies can interbreed to produce fertile offspring (Deharveng 1984b).
- *Type D* OTUs are 'splitter's species'. Morphological or other differences can be detected between type D OTUs, but these do not represent separate biological species status.

My own view is that taxonomists should be conservative in describing new species. Unless a series of specimens show constant and clear differences from previously described species, then it is better to consider them as a variety of an existing species until good evidence of likely reproductive isolation is obtained. Excessive splitting leads to confusion for users of identification keys, and an overestimate of true biodiversity.

5.2.2 Systematic methods

Almost all taxonomists now use cladistic methods for proposing relationships between taxa. This section examines the methods which have been used for examining the boundaries of species of Collembola, and relationships between them.

The different types of characters available are discussed in Sections 5.2.3, 5.2.4 and 5.2.5.

Attempts have been made by several authors to apply numeric and phenological cladistic methods (Forey *et al.* 1992) to study relationships between species. Numerous characters are selected (e.g. number of eyes, length of furca, etc.) and are entered into computer programs which then calculate the most parsimonious solution of all possible relationships between the species. Genera studied have included *Deutonura* (Deharveng 1989e), *Folsomia* (Hermosilla *et al.* 1984a), *Schaefferia* (Hermosilla *et al.* 1984b), *Bonetogastrura* and *Typhlogastrura* (Hermosilla *et al.* 1985), and species from the families Entomobryidae and Tomoceridae (Lee and Park 1991).

In most cases, the conclusions reached using these cladistic methods agree with those obtained from more traditional morphological studies (Lee 1985b). Where more detailed analysis is useful is in separating species within species groups. Where it is suspected that more than one species is present, a simple correlation between two characters may be sufficient to separate them (Figs. 5.2, 5.3).

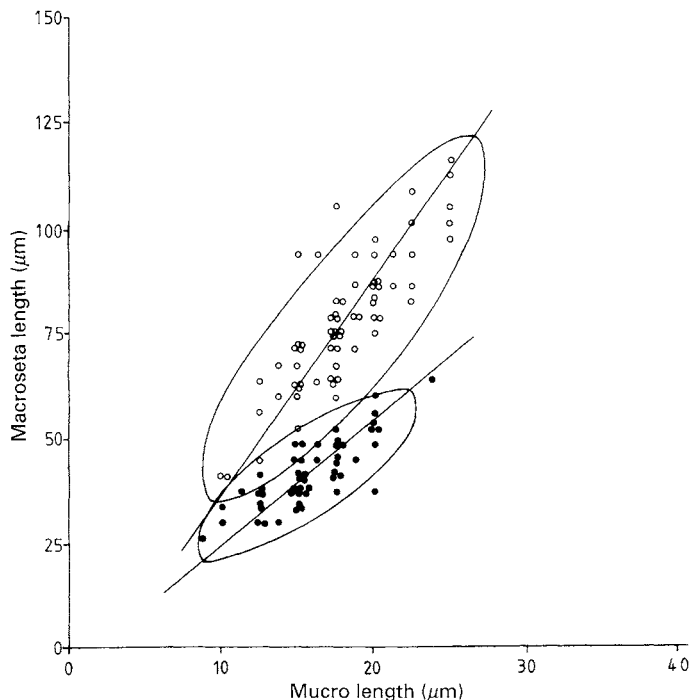


Fig. 5.2. Relationship between terminal abdominal macroseta length (character 18 : Fig. 5.3) and mucro length (character 10: Fig. 5.3) showing major axes and 95% confidence ellipses of populations of *Folsomia* sp. (Isotomidae) from several European localities (mainly Britain). There is reasonable evidence that two species are present, *F. manolachei* Bagnall (closed circles) and *F. quadrioculata* Tullberg (open circles). Reproduced from Wetton (1987) by kind permission of the author and the Royal Entomological Society of London.

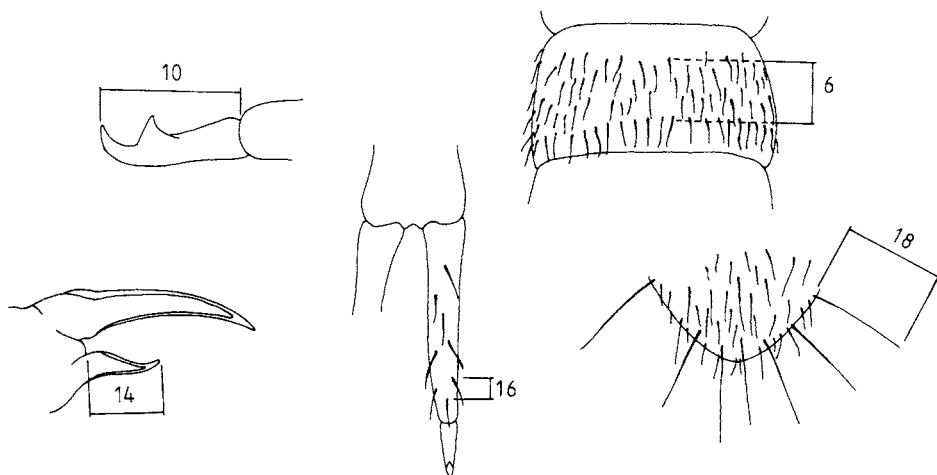


Fig. 5.3. The five most useful characters of the 21 features examined by Wetton (1987) in attempts to clarify species boundaries within *Folsomia* (Isotomidae). Character 6, abdominal segment 3 length; character 10, mucro length; character 14, empodium length on third leg; character 16, distance between terminal and outer subterminal dental setae; character 18, abdominal segment 6 terminal macroseta length. Reproduced from Wetton (1987) by kind permission of the author and the Royal Entomological Society of London.

However, in more complicated situations, techniques such as principal components analysis may have to be used to search for correlations between the states of a wide range of characters (see Quicke 1993 for details of the methodology). Pitkin (1980) used such techniques to separate species within the *Protaphorura armata* 'group' (Fig. 5.4). Similar methods have also been applied to species groups within other Onychiuridae (Mateos and Arbea 1986), Hypogastruridae (Arbea and Jordana 1990c) and Isotomidae (Mendonca and Dosreis 1991; Wetton 1987).

A major problem facing systematicists is the identification of homoplasy, and even resurrection of 'lost' genes. Marshall *et al.* (1994) have calculated that there is a significant probability over evolutionary timescales of 0.5–6 million years for a successful reactivation of silenced genes or 'lost' developmental programs. Thus in situation where rapid evolution has taken place (e.g. speciation on oceanic islands), it may be very difficult to reconstruct evolutionary pathways if the same character has disappeared then reappeared in successive species. The reactivation of long (>10 million years) unexpressed genes and dormant developmental pathways is not possible unless function is maintained by other selective constraints (Marshall *et al.* 1994).

5.2.3 Biochemistry and genetics

Comparative external morphology is still the main approach used in collembolan taxonomy (Section 5.2.4). Nevertheless, several authors have analysed properties of the products of genes such as enzymes (see below), or in the case of

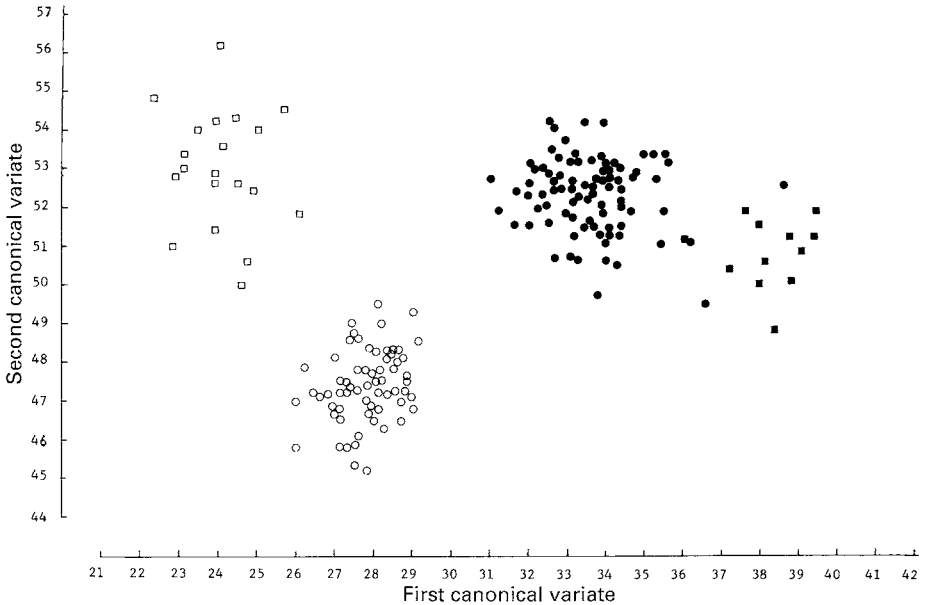


Fig. 5.4. Plots of individual scores in terms of first and second canonical variates following analysis of 21 characters in 298 female specimens of *Protaphorura armata* 'group' (Onychiuridae) collected from 14 sites in England and Wales. Four groups can be recognised which Pitkin (1980) regarded as probably representing *P. armata* (Tullberg) (○), *P. humata* (Gisin) (□), *P. aurantiaca* (Ridley) (●) and *P. quadriocellata* (Gisin) (■). Reproduced from Pitkin (1980) by kind permission of the author and the Royal Entomological Society of London.

Neanuridae, the chromosomes themselves (Prabhoo 1987). However, it should be pointed out that a major disadvantage of this type of taxonomy is that because springtails are so small, the specimen has to be damaged or even completely destroyed to obtain the information.

The salivary glands of some Neanuridae contain polytene or 'giant' chromosomes formed from lateral duplication of their DNA (Lee 1982, 1985a). The duplication provides many copies of the genes which transcribe the code for the manufacture of salivary enzymes and presumably increase their rate of synthesis. The animals pour these enzymes on to the food to form a colloidal suspension which is then drawn back into the mouth cavity (Cassagnau 1968a; Lee 1981). The chromosomes appear banded with light and dark regions which can be seen easily in the light microscope (Cassagnau 1971e; Figs. 5.5, 5.6). It is possible that polytene chromosomes may have evolved independently in different neanurid lines (Lee 1980a,b).

The banding patterns of the chromosomes may provide interesting information on geographic variation within species and genera (Cassagnau 1990b, 1993a, 1993b; Cassagnau and Deharveng 1980, 1981; Cassagnau *et al.* 1979; Dallai and Fanciulli 1982; Dallai *et al.* 1983). Differences in the structure of the chromosomes can often be found in specimens of the same species from different places

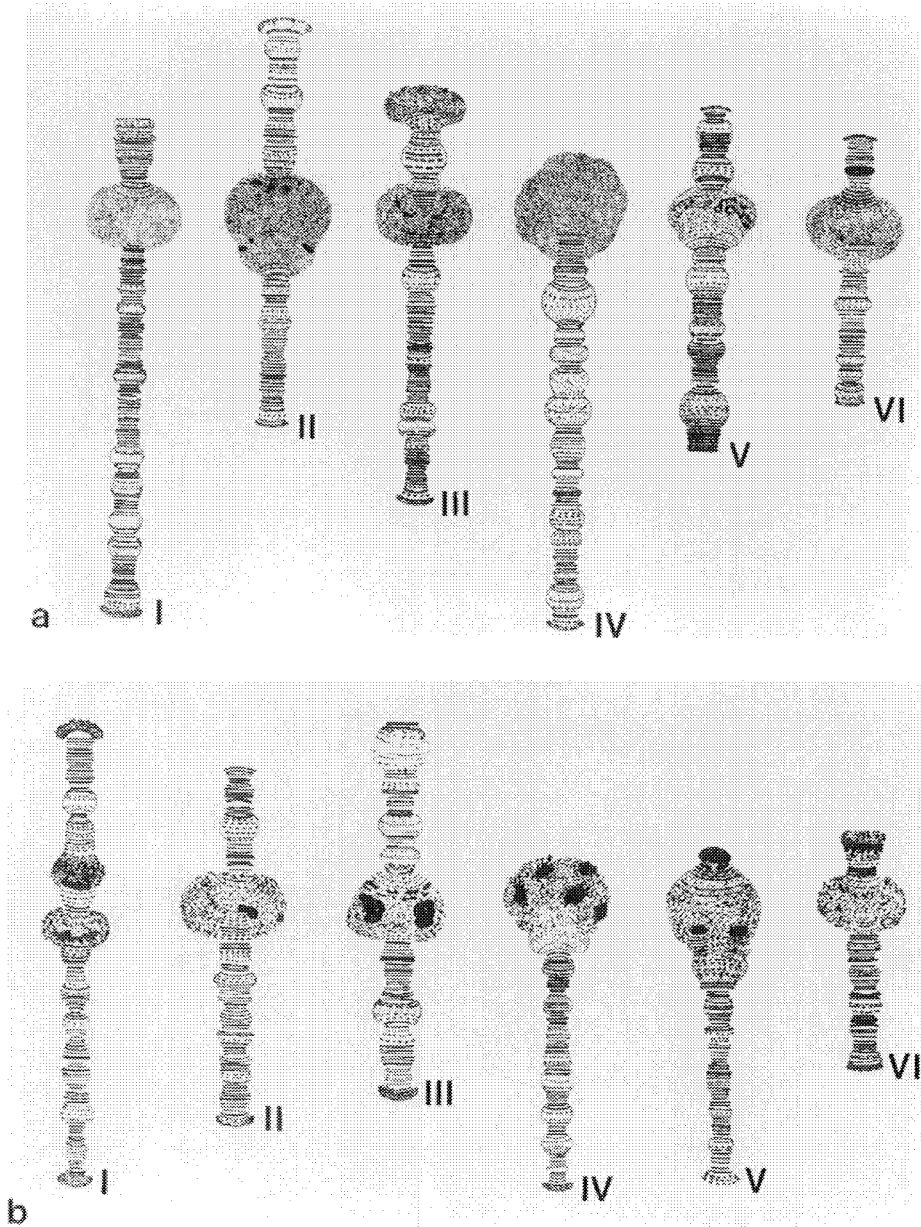


Fig. 5.5. Diagrams of karyotype 1 (a) and karyotype 2 (b) of chromosomes from the salivary glands of *Lathriopyga longiseta* (Neanuridae) collected from the Astroni crater, Naples, Italy. Karyotypes 1, 2 and 3 (not shown) comprise 60%, 30% and 10% of the population respectively; all exhibit the same external morphology. Reproduced from Fanciulli *et al.* (1989) by kind permission of the authors and the University of Siena.

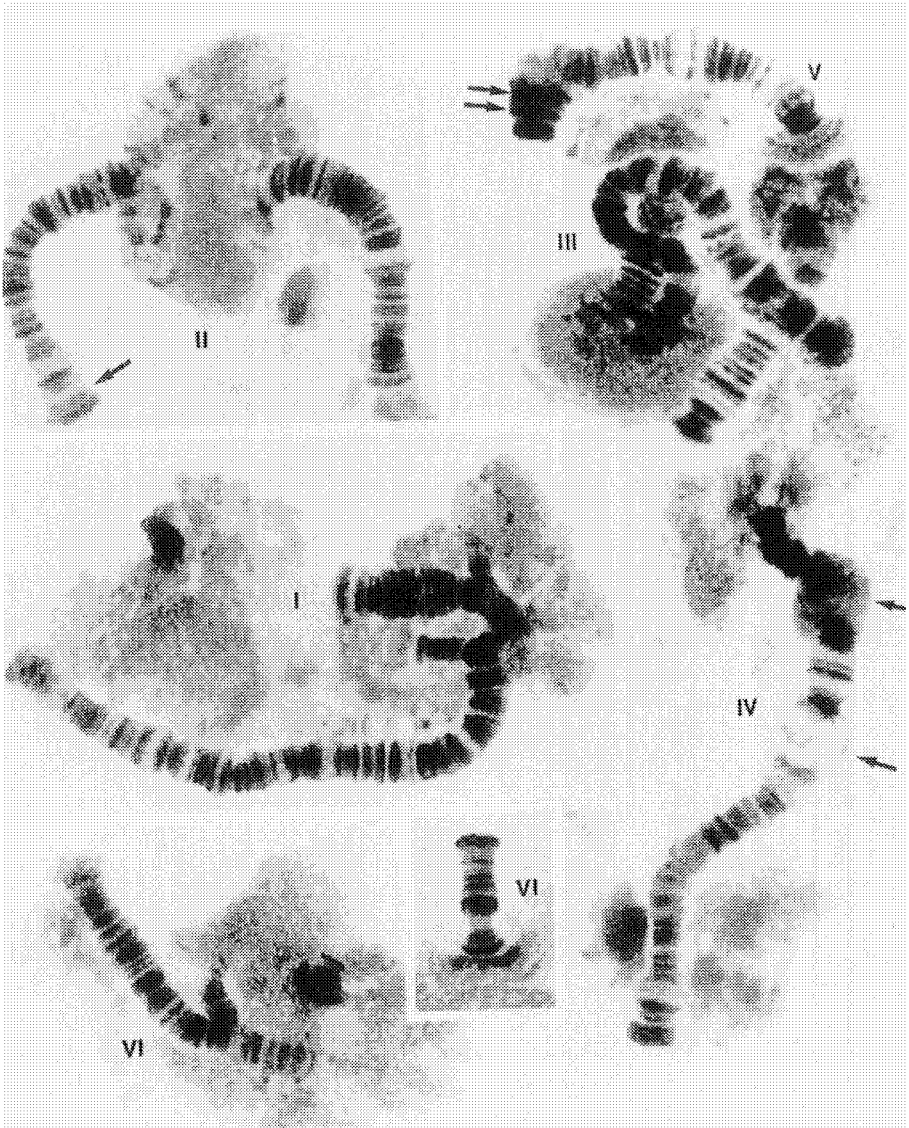


Fig. 5.6. Light micrograph of karyotype 1 of *Lathriopyga longiseta* (Neanuridae) (cf. Fig. 5.5a). Reproduced from Fanciulli *et al.* (1989) by kind permission of the authors and the University of Siena.

even though they share the same external morphology (Cassagnau 1974*b*, 1975, 1976; Deharveng 1976*b*, 1982*f*; Figs. 5.5, 5.6). These so-called 'chromosomal races' are a major problem for collembolan taxonomists (Fanciulli *et al.* 1989, 1991*b*). Indeed, Cassagnau and Lee (1982) and Cassagnau *et al.* (1985) came to

the conclusion that only external characters allowed satisfactory phylogenetic reconstruction and that information on chromosomal structure should be treated with care.

Biochemical 'fingerprints' are potentially useful for characterising different populations of a morphospecies which it is suspected may merit separate species status (Dalens 1982; Dalens and Najt 1981; Fanciulli *et al.* 1994; Hale and Rowland 1977; Prabhoo 1987). The method may also provide evidence of the beginnings of speciation (Dallai *et al.* 1986; Fanciulli *et al.* 1985, 1991a), and can be used to estimate rates of gene flow between populations (Fрати *et al.* 1994).

One of the most widely used techniques is allozyme analysis (Fрати *et al.* 1989; Lee and Park 1991). Allozymes are forms of the same enzyme which differ in their sequences of amino acids. Electrophoresis is used to separate allozymes according to their net charge and molecular weight. Those migrating different distances in the electric field usually differ by at least one amino acid. Since the amino acid sequence in proteins is related to the sequence of bases in DNA, differences between the allozyme 'fingerprint' of individuals, or pooled samples from specific populations, may reflect differences in the genes. The method has been used to show differences in allozyme status between morphologically indistinguishable, but geographically isolated populations of *Thaumanura ruffoi* (Fanciulli *et al.* 1986a), *Lathriopyga longiseta* (Fanciulli *et al.* 1986b), *Tetradontophora bielensis* (Fanciulli *et al.* 1991a), and to confirm the legitimacy of awarding species status to different colour morphs of *Orchesella* (Fрати and Szeptycki 1990; Fрати *et al.* 1992a,b, 1994).

However, care should be taken in reading too much into allozyme analysis. A number of factors may modify the rate at which the genes for particular proteins are expressed. 'Fingerprints' for certain enzymes such as esterases may change throughout a moult cycle (Dalens and Rousset 1986, 1988; Grimnes 1981, 1986), and some enzymes may migrate in an electrophoretic field in an identical fashion to others which have a different amino acid sequence.

Since the unit of natural selection is the gene, it is an attractive proposition to be able to look at nucleotide sequences of the DNA rather than the products of their expression. Unfortunately the genetic approach is at an early stage in Collembola (Fodde *et al.* 1986; Hwang *et al.* 1995; Soto-Adames *et al.* 1994). Only Carapelli *et al.* (1995a,b) have used DNA sequence divergence and allozyme differences to support taxonomic decisions at the species level. They showed that colour varieties of *Isotomurus palustris* (Cassagnau 1987) should probably be given separate species status.

What is desperately needed is more sequence data from collembolan DNA but the technical difficulties and problems of obtaining funding are likely to delay this for some years.

5.2.4 Morphology

The key question that collembolan taxonomists should ask is 'what degree of morphological difference between two individuals is evidence of reproductive

isolation and hence separate species status?'. In arthropods with complicated external genitalia such as millipedes (Hopkin and Read 1992), differences in the structure of these secondary sexual characteristics is convincing evidence that more than one species is involved. However, the genital openings of male and female Collembola are extremely simple and have been little-used in taxonomy (Betsch-Pinot 1974*a,b*; Fig. 4.1). One has to rely on other morphological features. The main problem with comparative morphology is character variability (this topic is covered in more detail in Section 5.3.2). In this Section, the taxonomic characters which have been most widely used are discussed. Those of particular relevance to Onychiurinae are covered in Section 5.4.

One of the clearest characters is body colour. In some species, the distribution of pigment is species-specific (Carapelli *et al.* 1995*a*; Frati and Szeptycki 1990), and has been used for separating juveniles of two species of *Heteromurus* which are otherwise morphologically identical (Bretfeld 1988). However colours often fade in preservative, and features such as interference colours arising from the refraction of light through body scales become impossible to see (Gisin and Gama 1962). Most identification keys therefore rely on characters that can be seen in preserved specimens.

The mouthparts may provide useful taxonomic information. The fine structure of the mandibular teeth (Wetton 1988), maxillae (Fjellberg 1976*c*, 1977*b*, 1984*b*; Fig. 5.7) labium (Hale 1966*b*; Massoud *et al.* 1975) and labrum (Eisenbeis and Meyer 1986; Szeptycki 1967*a*; Waltz and Hart 1995*c*; Yosii 1976*b*) reflect differences between species in diets and feeding behaviour.

The most widely used taxonomic method of all is known as *chaetotaxy* (Betsch *et al.* 1990; Deharveng 1979*b*; Massoud and Thibaud 1973; Nayrolles and Betsch 1993; Rusek 1986*b*; Yosii 1961). It is probably also the most controversial. The technique involves mapping the distribution of setae on the surface of the cuticle and looking for similarities and differences between species. The basic arrangement on the body segments is three parallel lines of simple setae called the a (anterior), m (median) and p (posterior) rows but these are often reduced (Yosii 1956*a*; Fig. 5.8). Smaller supplementary setae (plurichaetae) are not usually considered (Lobbes 1977). The arrangement of setae on the antennae, legs, ventral tube and furca may also be fundamentally similar across different groups (Lawrence 1977, 1978*a*). In Symphypleona, the fusion of segments has made it difficult to recognise a, m and p setae and there are differences of opinion on the best ways to describe setal positions (Betsch and Bretfeld 1991; Betsch and Waller 1994; Bretfeld 1994*b*). Many species have reduced numbers of setae on the body and appendages in comparison to the 'basic' condition and this information can be used to reconstruct probable evolutionary pathways (Fjellberg 1991*c,d*).

Whichever method is chosen, it is clear that for chaetotaxy to be of the greatest use in phylogeny, the positions, and structure and function (where this can be elucidated) and homology of all major setae on the head, thorax, abdomen and appendages should be determined (André 1988*a,b*, 1989*a*; Nayrolles 1995*a*). This is performed most satisfactorily with intact unmounted specimens whose position can be changed so that every part of the animal can be inspected. Chaetotaxic

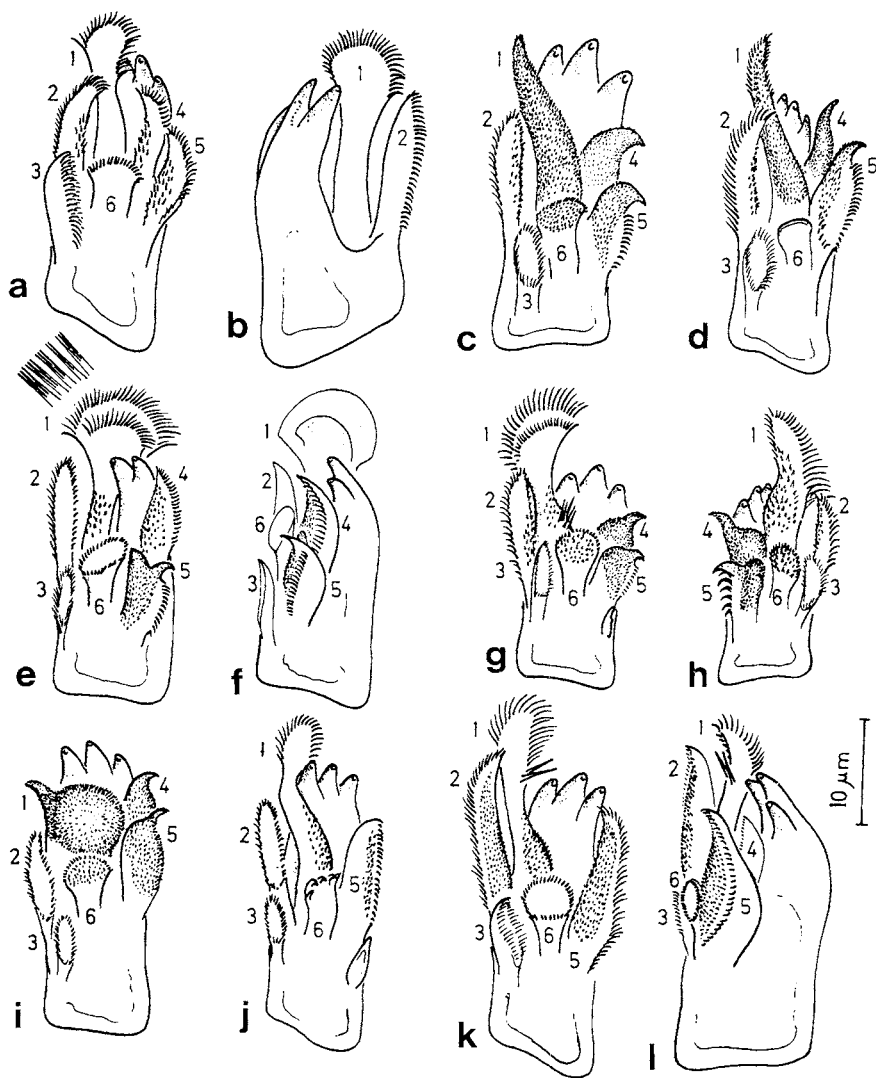


Fig. 5.7. Maxillary head of (a) *Podura aquatica* (Poduridae), inner side; (b) *Podura aquatica* outer side; (c) *Hypogastrura tullbergi* (Hypogastruridae); (d) *H. oregonensis*; (e) *H. manubrialis*, inner side with detail of marginal fringe on Lam. 1; (f) *H. manubrialis*, dorsal side; (g) *H. vernalis*; (h) *H. pannosa*; (i) *H. notha*; (j) *Mucrella acuminata* (Hypogastruridae); (k) *M. navicularis*, inner side; (l) *M. navicularis*, dorsal side. Reproduced from Fjellberg (1984c) by kind permission of the author and the Royal Zoological Society of Belgium.

descriptions of slide-mounted material, using methods such as those described by Bretfeld (1991) and Rusek (1974a, 1975b), do not allow movement of the specimen. Relative positions of setae may change due to pressure from the cover slip, or setae may be hidden by other structures.

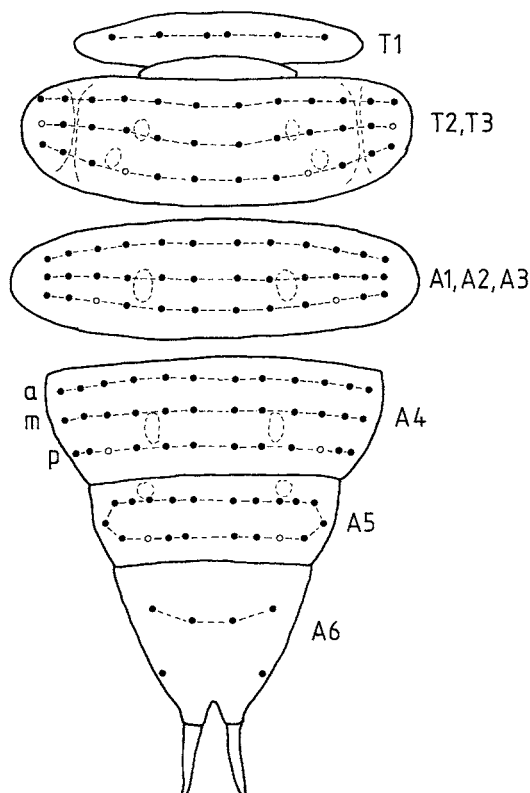


Fig. 5.8. Schematic diagram of the dorsal chaetotaxy of a 'typical poduromorphan' showing the 'basic arrangement' of three rows of setae (a, anterior; m, medial; p, posterior) on thoracic segments T2 and T3, and abdominal segments A1 to A4, and reductions on thoracic segment T1 and abdominal segments A5 and A6. Redrawn after Yosii (1956a) by kind permission of the author.

Complete chaetotaxy is extremely complicated (see Fig. 5.9). André (1988b) recorded the positions of more than 1000 'setiform organs' in his description of *Xenylla jocquei*. One only has to compare the 'traditional' redescription of *Sminthurus viridis* by Lawrence (1966) with the re-redescription of the same species by Nayrolles (1995c). The latter author included a table of appendicular chaetotaxy which, although necessary within the context of full chaetotaxic descriptions, takes some time to interpret fully (Fig. 5.10). Of course, keys do not have to include all this information. It should be possible with complete chaetotaxic descriptions to identify constant differences in a much smaller number of characters which can be used to separate species in identification guides.

The chaetotaxy of some species is remarkably similar over large geographic distances, e.g. *Cryptopygus bipunctatus* in North America and Europe (Bernard and Snider 1994). However, one problem with chaetotaxy is that while the positions of many innervated setae such as trichobothria and chemosensory organs are

probably under direct genetic control, smaller setae may develop in 'fields' so that their exact number and position varies between individuals of the same species (Lucianez and Simon 1993*b*).

Further information on the use of chaetotaxy in systematic studies can be found in the following publications on Brachystomellidae (Mendonca and Arlé 1992), Hypogastruridae (Bonnet *et al.* 1973; Deharveng and Bourgeois 1991; Hüther 1962; Yosii 1962), Neanuridae (Deharveng 1981*c*, 1991; Deharveng and Bedos 1991; Fjellberg 1985*c*; Greenslade and Deharveng 1990; Grow and Christiansen 1974; Palacios-Vargas 1986; Potapov and Banasko 1985), Onychiuridae (Jordana and Arbea 1994; Lucianez and Simon 1992*b*; Snider 1977), Entomobryidae (Arbea and Jordana 1990*d*; Barra 1975*a*; Gisin 1963*a*; Mateos 1993; Snider 1967*b*; Szeptycki 1967*a*, 1969, 1972, 1979), Isotomidae (Deharveng 1977; Deharveng and Lek 1993; Grow and Christiansen 1976; Potapov 1989), Oncopoduridae (Szeptycki 1977*a*), Paronellidae (Mittra and Dallai 1980), and Sminthuridae (Betsch and Waller 1989; Itoh 1994*b*; Nayrolles 1988, 1989*b*, 1990*a,b,d*, 1991, 1992, 1993*a,b,c*, 1994*a,b,c*, 1995*a,b,c*; Weiner and Betsch 1992).

5.2.5 Ecology and behaviour

Miller and Wenzel (1995) have argued that ecological and behavioural characters can be used to support taxonomic decisions based on morphology. The similar ecology and identical mating behaviour of *Deuterosminthurus bicinctus* and *Deuterosminthurus flavus* led Ellis (1973) to conclude that only one species was involved which he united under the name *Deuterosminthurus bicinctus*. Ecophysiological differences have also been observed between morphologically similar species of *Folsomides* (Poinsot-Balaguer and Barra 1982). Pomorski and Weichsel (1993) demonstrated species-specific 'nest' building behaviour of closely-related species of *Hymenaphorura*. However, while such observations provide useful supporting evidence for taxonomists, they are unlikely to replace traditional descriptive methods which rely on examination of dead material.

5.3 Problems of defining species boundaries

5.3.1 Introduction

The biological species concept is genetically based. It assumes zero gene flow between individuals of separate species. However, the external morphology of Collembola is a result of the interactions between the products of their genes and their environment. It is therefore possible for two individuals of the same species with identical genes to be morphologically different. An analogy may help to explain this situation.

Take for example the robots which paint cars in automobile manufacturing plants. The computer program which controls the actions of the robots is analogous to the genes in a springtail. The colour of each car will depend on the paint which is loaded into the robot, even though exactly the same instructions for

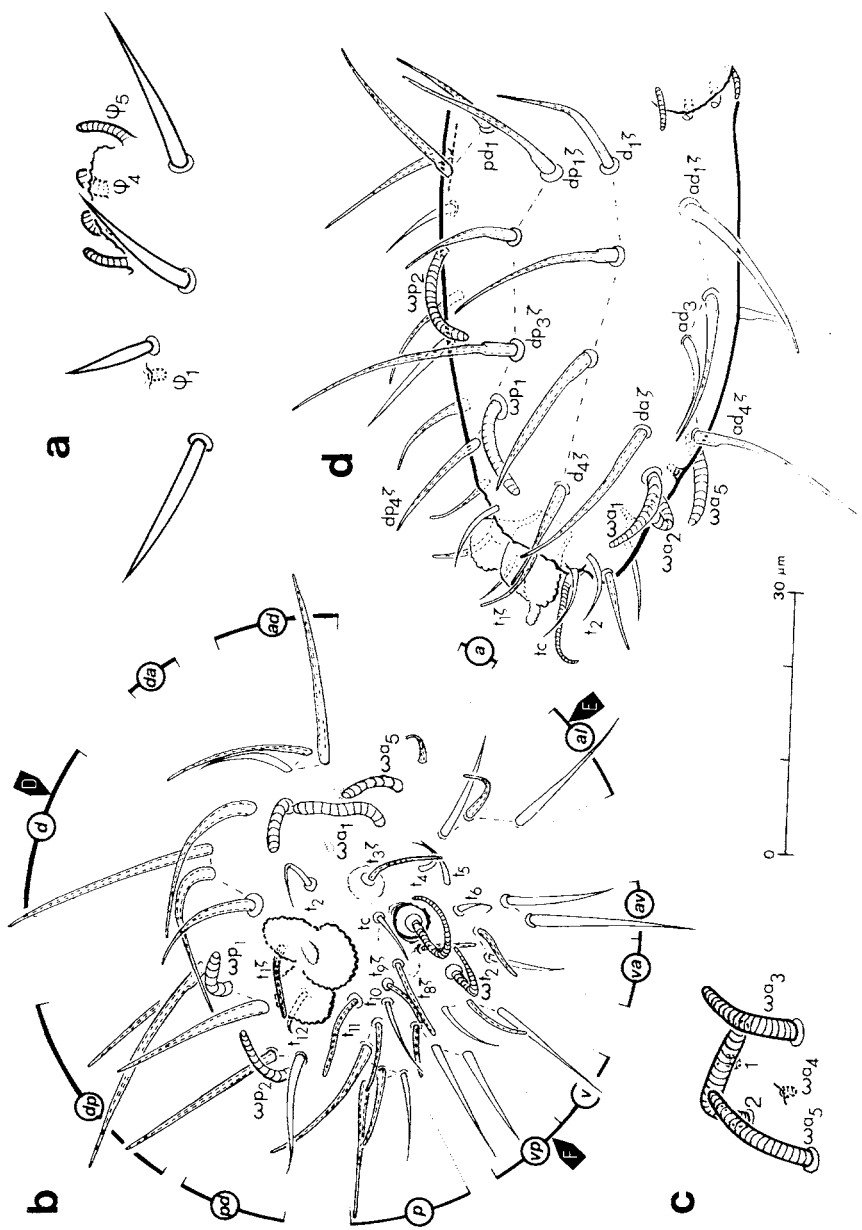


Fig. 5.9. Diagram of the distal part of the antenna of *Xenylla jocqueti* (Hypogastruridae) showing the complex arrangement of 'setiform organs'. (a) Sensory complex on segment 3; (b) end-on view of segment 4 divided into 12 sectors (*d*, *da* etc); (c) dorsal view of the antiaxial group of solenidia of segment 4; (d,e,f) three lateral views of segment 4 (orientations shown as black arrows D,E, and F respectively in (b). Reproduced from André (1988b) by kind permission of the author and Editions AGAR.

AP	Δ	—									
AD	Π	—									
	Δ	D: i0 T: e+1, a+1, i+1, pi+1, pe+1 Q: p+1, i+2 i0, i+1, i+2, and a+1 are small and slender setae on large base.									
AT	Π	—									
	Δ	Other setae: Q: p+2									
			Ge	Gae	Ga	Gai	Gi	Gpi	Gp	Gpe	
		Setae -1		T	Q	T	Q	T	Q	T	
		Setae 0		D	D	D	D	D		D	
		Setae +1		T	T	T		D	T		
		Be, Bae, Ba, Bai, and Bp become macrochaetae during development.									
AQ	str	B completely zoned. Section M euwhorled with 14 or 15 whorls. Right euwhorlation. Subsegmentation formula: 1 + 14/15 + 1 = (A) + (M1,14/15) + (B) with BA more or less well individualized as a subsegment. Right subsegmentation.									
	A	Π	Alipi								
		H	Allleae, Alllpe								
		Δ	Apical bulb: joined to the apex Subapical organ: medium-sized, clavate D: Alai Alllpe is a blunt microchaeta.								
	M & B	H	Heae does not reach BA. For <i>Heae*</i> : <i>m</i> = 9.3; min = 7; max = 11. For <i>Hppe*</i> : <i>m</i> = 10.8; min = 9; max = 14. For <i>h*</i> : <i>m</i> = 10.0; min = 9.0; max = 11.0.								
		G	Setae of BB: P: BBae, BBpe Q: BBae, BBp / BA with 2 variable setae / n80%(BM) = 9-15 / n80%(B) = 20-26 / some cases of absence of G setae on M / n80%(G) = 157-169.								
SB	prc	—									
	Δ	P: 1 seta									
SA	Δ	—									
	Δ	P: 1 seta									
CX	Δ	P: i1									
	Δ	P: ae, i1, ms T: a, Oi1									
TR	Π	—									
	Δ	Q: pi									
	Δ	T: a2, Oi1, Oi2 Q: ae									
FE	Π	—									
	Δ	T: pi2, p2, pe2, pe3 Q: a2, Op									
	Δ	T: a5, ai2, pe2 Q: a2, ai5, pe3, Op									
	Δ	T: a5, ai2, pe2 Q: a2, ai5, pe3, Op (Q)C: ai3 (oc = 0.7), ai4 (oc = 0.8)									
TI	V	—									
	K	—									
	FP	—									
	Δ	T: 4ai1, 4pi1, Vai, Vpi, Fsa, FSpe↓, O1pe, O2pe, O3pe, O4pe (T)Q: 3a (oc = 0.8), 3p (oc = 0.6), 4a1 (oc = 0.5) Q: 2ae, 3ae, 4ae1, 4p1, 4ai2, 4pi2, FSe↑, FSai, FSpi, O1ae									
	Δ	T: 4ai1, 4i1, Vai, Vpi, Fsa, FSpe↓, O1pe, O2pe, O3pe, O4pe (T)Q: 3a (oc = 0.8), 3p (oc = 0.5), 4a1 (oc = 0.6) Q: 2ae, 3ae, 4ae1, 4pi1, 4ai2, 4pi2, FSe↑, FSai, FSpi, O1ae (Q): 4p1 (oc = 0.5)									
	Δ	T: 2a, 3a, 3ai, 3i, 4ai1, 4i1, Vai, Vpi, Fsa, FSpe↓, O1pe, O2pe, O3pe, O4pe (T)Q: 2p (oc = 0.5), 3p (oc = 0.2), 4a1 (oc = 0.7) Q: 2ae, 3ae, 3pi, 4ae1, 4pi1, 4ai2, 4pi2, FSe↑, FSai, FSpi, O1ae									
MA	Π	—									
	Δ	T: a1, pe2 Q: pe3									
DE	Δ	Other setae: P: 1p T: 3p, 4p, 5p Q: BBpi oc(Via) = 0.7									
			Ge	Gae	Ga	Gai	Gi	Gpi	Gp	Gpe	
		Whorls I to VI	I	P	P	P	P	P	P	P	
			II		P	P	P		P	P	
			III			P	P		P	P	
			IV			P	P		T	P	
			V			P	P		T	P	
			VI				(P)		Q	T	
		Whorl B		T		P			P	P	
MU	Δ	Chaetotaxy: D: mu Morphology: anterior lamella double, outer and inner lamellae smooth.									

Fig. 5.10. Chaetotaxy of the antennae (top box), legs (middle box) and furca (bottom box) of *Sminthurus viridis* (Sminthuridae). Reproduced from Nayrolles (1995c) by kind permission of the author and Artis Bibliotheek, University of Amsterdam.

movement of the spray gun are sent in every case. Some of the components of the pigments which give Collembola their colour are derived from the food (South 1961). Thus, it is possible for two genetically identical springtails to be different in colour if they have fed on different diets. Furthermore, the robot may run out of paint but continue to go through the motions of spraying. If pigments are not available in the food of springtails, then the animals may have very weak colouration.

Identical painting conditions may result in different qualities of paint finish so that a cold factory produces a less shiny finish than a warm one. Thus, the development of certain morphological features of genetically identical Collembola may be affected by local climatic conditions. For example, Hale (1996*b*) showed that the shape of the thorax of *Lepidocyrtus lignorum*, an important taxonomic character, changed with altitude even though other features such as chaetotaxy of the labium stayed the same. Fritzlar *et al.* (1986) found specimens of *Orchesella* and *Entomobrya* to be of different colour near a source of phosphate pollution in comparison to the same species from uncontaminated sites.

These examples show that there is not necessarily a direct association between genes and external morphology. The major problem for collembolan taxonomists is determining the relationship between morphospecies and biological species. In the following two Sections, some of the reasons for these difficulties are outlined.

5.3.2 Variability of morphology within a species

The basic requirement for successful taxonomy is a series of well-preserved, undamaged adult specimens. However, there are numerous examples of new species being described from incomplete or poorly preserved animals (Lawrence 1968), and in some cases from a single individual. For example *Paronychiurus paxi* (described from one specimen by Stach in 1939) was shown by Pomorski (1990*a*) to be a juvenile of a species described by Stach in 1934. This practice should obviously be discouraged (Petersen 1965). Abnormalities due to disease, or faulty development, are not uncommon in Collembola (Miles 1975; Palacios-Vargas 1979; Rapoport 1962*c*). Shan-Xiang (1980) went so far as to describe a new subfamily of Onychiuridae with the diagnostic feature of a double sensory organ on the third antennal segment. Unfortunately the description was based on moulting specimens just before they sloughed off the old cuticle.

The scanning electron microscope (SEM) is important for taxonomy but for reasons of cost has been relatively little used in comparison to more traditional light microscopy. This is a shame because there are many characters such as the shape of the foot claws (Massoud and Vannier 1965*b*) which provide much more information if considered as three-dimensional structures instead of two-dimensional slide mounts. The higher resolution of the SEM reveals many features not visible at lower magnifications (Eisenbeis and Wichard 1987; Hale 1969).

Care must be taken to preserve specimens in a form which ensures their long-term integrity. This is particularly important for type specimens which should be deposited in accessible collections where their existence can be recorded (Mari Mutt 1978*b*; Sartori 1991; Vilkamaa 1988*a*). Unfortunately, several of the slide

mountants which were recommended in earlier years (e.g. Gisin 1968) have not stood the test of time and have degraded badly (Greenlade and Sutrisno 1994; Upton 1993; Waltz and McCafferty 1984). In addition, many springtails in old 'spirit' collections are in poor condition because they were preserved in unsuitable liquids or have dried out (Loring and Snider 1983). Others, including type specimens, have been destroyed through fire or war and have to be redescribed from modern material (Salmon 1974a).

One of the easiest errors to make is to give separate names to males and females of the same species (Ellis 1975), or to describe a new species or genus from juveniles of an existing species (Fjellberg 1974c; Gough 1973a; Pomorski 1990a). Thus the genus *Architomocerura* described by Denis in 1931 was shown by Goto (1956) to be an immature stage of *Tomocerus* Nicolet 1841. Lawrence (1978c) showed that different growth stages of *Cryptopygus fasciatus* had each been given a name and that the species had been assigned to no less than nine genera. Species which undergo epitoky, cyclomorphosis or ecomorphosis (Section 8.6) change their appearance at certain times of the year (Bourgeois 1974; Cassagnau and Izarra 1969; Fjellberg 1976d; Hart and Waltz 1995; Leinaas 1981c; Waltz and Hart 1985; Zettel and Zettel 1994b). Different forms of the same species can be described as new unless this phenomenon is recognised. For example, the genus *Spinisotoma* described by Stach (1926) was shown subsequently to be an epimorphic form of *Isotoma* (Cassagnau 1956; Stach 1961).

Some species show inter-individual variation in numbers of ocelli in the eyes (Christian 1983; Christian and Schaller 1982; Lawrence 1959; Wetton 1987), shape of the mucro (Goto and Ögel 1961; Fig. 5.11) and colour (Lawrence 1961a). The external appearance may also be affected if the springtail is heavily parasitized (Ellis 1974c). All these examples have resulted in many cases of synonymy, some of which have still to be resolved. Excessive splitting of taxa on the basis of minor differences in morphology or colour may result in the same biological species having more than one name. This is compounded if the same species is described independently by taxonomists in different countries. For example, the common and widespread collembolan *Entomobrya nivalis* (Linnaeus, 1758) was described under at least 81 species and subspecies names before 1960 (Salmon, 1964). Modern communications and the relative ease of international travel should help to minimise this problem in the future.

5.3.3 Human 'error'

If someone performs a bad scientific experiment and the results find their way into the literature, then they can be ignored. However, in taxonomy, once someone gives a name to a new 'species', it is recorded in the Zoological Record and is recognised until someone synonymises it with a previously described taxon. In my opinion, there are several genera which contain more morphospecies than biological species. Some examples within Onychiurinae are given in Section 5.4.

There is no doubt that questionable taxonomy has been published, and that some workers have taken the process of splitting taxa to extremes. It is unfortu-

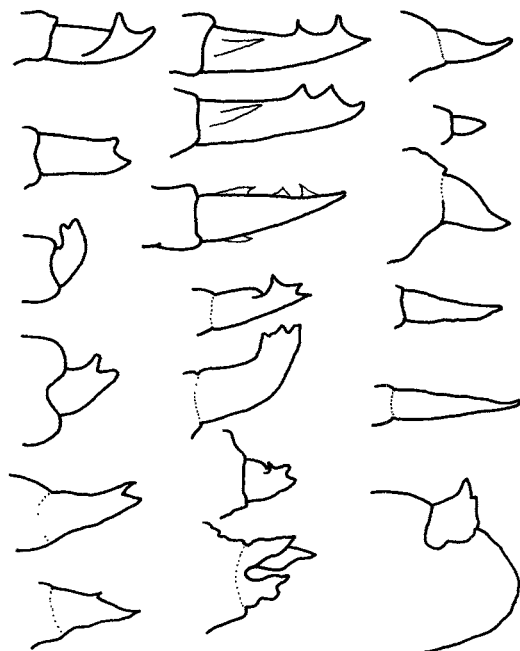


Fig. 5.11. Individual variation in the shape of the mucro in laboratory cultures of *Folsomia candida* (Isotomidae). Redrawn after Goto and Ögel (1961).

nate that some of a present day taxonomist's time is spent sorting out the confusion resulting from poor taxonomy of the past (Goto 1955a). While most new species are clearly valid, some are still erected on the basis of very subtle character differences. Modern taxonomists should think very carefully of the future implications of adding another name to the literature unless they are convinced that a true biological species is involved (Lawrence 1979). Commendable restraint has been shown by Beruete *et al.* (1994) and Dunger (1976a) who are waiting to assign specific names to possible new species of *Onychiurus* until more specimens are found. R.J. Snider collected a single specimen of what he suspected was a new species in 1960, but he waited 23 years until more specimens turned up before describing it as *Sminthurus mendenbergae* (Snider 1983b).

Many early descriptions of new species were very brief and most had no illustrations (e.g. Ridley 1880). Even a worker such as Stach, who made profound contributions to collembolan taxonomy, could miss important features of his specimens (Gough 1973c; Pomorski and Skarzynski 1989). Of course, it is easy to make mistakes. Nevertheless, some workers are renowned for their lack of scientific rigour. For example, Bellinger (1985b) examined H.G. Scott's reference collection of Collembola in the USA (see Roback 1981) and found that only 24 of the specimens were certainly, and another 20 possibly, correctly identified. Of the remainder, 109 were placed in the wrong genus and 7 others in the wrong family.

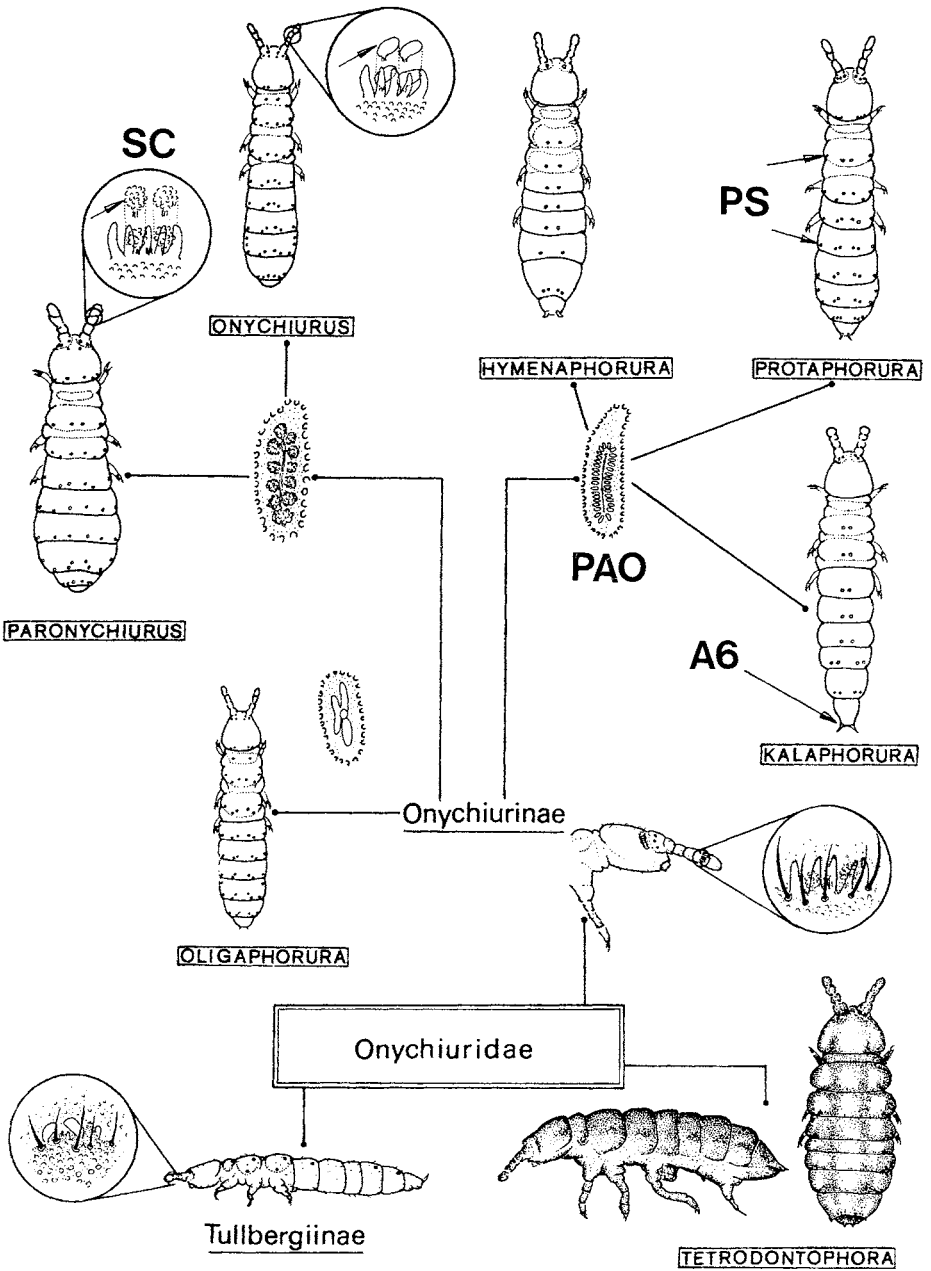


Fig. 5.12. Flowchart for separating Polish subfamilies and genera of Onychiuridae. The main characters used are structure of the postantennal organ (PAO) and sensory complex on the third antennal segment (SC), presence or absence of lateral pseudocelli (PS) and the shape of the sixth abdominal segment (A6). Note that *Oligaphorura* is considered to be synonymous with *Archaphorura* in Appendix A. Reproduced from Pomorski and Skarzynski (1992) by kind permission of the authors and Biologica Silesiae, Poland.

The British entomologist R.S. Bagnall described numerous new species of Collembola in the 1930s and 1940s, especially Onychiuridae (e.g. Bagnall 1935, 1937, 1947, 1949). While some of these species of onychiurids are recognised as 'good', many have been synonymised (Choudhuri 1963; Salmon 1959). Goto and Delamare-Deboutteville (1953, 1954), Lawrence (1961*a*, 1962, 1963*b*, 1973*b*) and Lawrence and Goto (1968) came to similar conclusions regarding many other of Bagnall's 'species'.

5.4 The Subfamily Onychiurinae

The Onychiurinae are small, blind, poorly pigmented euedaphic Collembola which live permanently in the soil or under stones and rotting wood on the soil surface. They have lost the springing organ (Figs. 5.12, 5.13), and are unable to jump, although traces of a furca are present in some species. The world list of Bellinger and Christiansen recognises nine genera (Appendix A). Most of these used to be considered as subgenera of *Onychiurus* but the modern view is that they should be given generic status.

Three rare genera of restricted distribution, namely *Ongulonychiurus*, *Probolaphorura*, and *Uralaphorura*, described in the papers of Thibaud and Massoud (1986*b*), Dunger (1976*a*) and Martynova (1978) respectively, are fairly atypical onychiurids and their taxonomic position is uncertain. The remaining six genera are *Archaphorura* (incorporating *Dimorphaphorura*, *Micraphorura* and *Oligaphorura*, all described by Bagnall in 1949), *Hymenaphorura*, *Kalaphorura*, *Onychiurus*, *Paronychiurus*, and *Protaphorura* (incorporating *Allaphorura*, also described by Bagnall in 1949). These are much more common and widespread and are separated on the basis of the structure of the postantennal organ (PAO) and sensory organ on the third antennal segment, distribution of pseudocelli on the body (Pomorski and Skarzynski 1992; Fig. 5.12, 5.13), and presence or absence of a vestigial furca. Not all taxonomists agree with this arrangement (e.g. Kaprus and Weiner 1994, 1996; Weiner 1986*a*, 1994; Fig. 5.12) but I have followed Bellinger and Christiansen's view in Appendix A to minimise confusion for those consulting their electronic list.

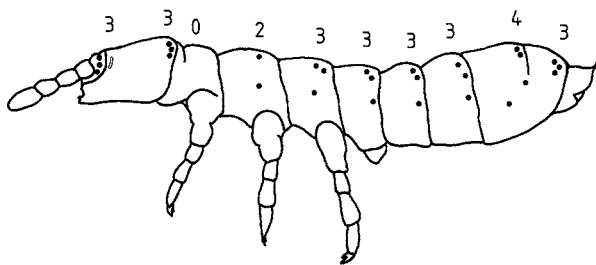


Fig. 5.13. Semi-schematic diagram showing the positions of pseudocelli on the left side of *Protaphorura armata* (Onychiuridae). The pseudocelli formula is 33/023/33343. After Gisin (1960*a*) and others.

At the species level, there is considerable disagreement on the status of many taxa. For the purposes of this discussion, I shall focus on the genus *Protaphorura* which was formerly considered as a subgenus of *Onychiurus*. Of the 143 species of *Protaphorura* regarded as valid by Bellinger and Christiansen (Appendix A), 89 were described before 1969, 26 between 1970 and 1979, 18 between 1980 and 1989, and ten since 1990. Of the 334 'species' of Collembola on the official British list (Gough 1978; Kloet and Hincks 1964), 39 are in *Protaphorura* (Table 5.1). Within *Protaphorura*, several characters have been used to separate species, the main ones being the presence, absence or positions of setae (chaetotaxy), and the numbers and arrangement of pseudocelli on the anterior and posterior parts of the head, and segments of the thorax and abdomen. The latter give the so-called 'pseudocelli formula' (Fig. 5.13).

Until the 1930s, relatively few species were recognised in Onychiurinae. However Bagnall, and subsequently Gisin, described numerous new species from Britain and elsewhere in Europe, many on the basis of minute differences in chaetotaxy and pseudocelli formula (for examples see Bagnall 1935, 1937, 1947, 1949; Gisin 1960*a,b,c*, 1961*a*, 1962*c*, 1963*a,b,d*, 1964*a,b*). A glance at Table 5.1 illustrates the impact that these two workers had on the British list alone. Gisin's approach has been criticised by several taxonomists including Bödvarsson (1959; 1970*a*), Böhle (1991), Pitkin (1980) and Pomorski (1986).

Problems arising from synonymy were highlighted by Pomorski (1990*c*) who studied variations in the pseudocelli formula and chaetotaxy in laboratory cultures of *Protaphorura*. Confining ourselves to species of *Protaphorura* on the British list (Table 5.1), Pomorski (1990*c*) considered the following to be 'good' species (with synonyms in brackets):

P. pannonica Haybach 1960 (= *P. trinotata*)

P. subuliginata (= *P. subarmata*)

P. armata (= *P. nemorata*, *P. humata*, *P. tricampata*)

P. campata (= *P. procampata*)

P. meridiata (= *P. pulvinata*)

P. aurantiaca (= *P. uliginata*, *P. lata*, *P. prolata*, *P. sublata*).

In other words, of the original 17 'species' he examined, only 6 remain valid.

However, the use of Gisin's pseudocelli formula for 'splitting' species of Onychiurinae has been supported to some extent by Fjellberg (1980*a*), Salmon (1959) and Skarzynski (1991). In fact Hale (1964*b*, 1965*d*, 1968, 1969, 1980) reported that several of Gisin's 'species' breed true in laboratory culture, although the validity of his experimental approach has been questioned by some (e.g. Bödvarsson 1970*a*). A word of warning, however. It is of course possible for two morphological varieties of the same species to breed true in culture if they are kept separate, even though they are not reproductively isolated in the wild.

Lawrence (1979) has pointed out that if all mathematically possible combinations of the characters used by Gisin were to exist, then more than 100 000

Table 5.1. Species of Genus *Protaphorura* Absolon, 1901 recorded from Britain in the check list for Collembola of Kloet and Hincks (1964) and the update of Gough (1978) and others. The 24 species regarded as valid by Bellinger and Christiansen in their world list (see Appendix A) are shown in bold type. Those not shown in bold are probable synonyms following revisions by Bödvarsson (1970a), Pitkin (1980), Pomorski (1990c) and others. However, there is no widespread agreement among taxonomists as to how many of the 39 'species' on this list should be considered as true biological species.

-
1. *Protaphorura alborufescens* (Vogler 1895)
 2. *Protaphorura artica* (Tullberg 1876)
 3. *Protaphorura armata* (Tullberg 1869)
 4. *Protaphorura aurantiaca* (Ridley 1880)
 5. *Protaphorura bagnalli* (Salmon 1959)
 6. *Protaphorura bicampata* (Gisin 1956)
 7. *Protaphorura caledonica* (Bagnall 1935)
 8. *Protaphorura campata* (Gisin 1952)
 9. *Protaphorura debilis* (Moniez 1890)
 10. *Protaphorura evansi* (Bagnall 1935)
 11. *Protaphorura fimata* (Gisin 1952)
 12. *Protaphorura flavidula* (Bagnall 1939)
 13. *Protaphorura furcifera* (Börner 1901)
 14. *Protaphorura halophila* (Bagnall 1937)
 15. *Protaphorura hortensis* (Gisin 1949)
 16. *Protaphorura humata* (Gisin 1952)
 17. *Protaphorura imminuta* (Bagnall 1937)
 18. *Protaphorura lata* (Gisin 1956)
 19. *Protaphorura magnicornis* (Bagnall 1937)
 20. *Protaphorura meridiata* (Gisin 1952)
 21. *Protaphorura nemorata* (Gisin 1952)
 22. *Protaphorura octopunctata* (Tullberg 1876)
 23. *Protaphorura procampata* (Gisin 1956)
 24. *Protaphorura prolata* (Gisin 1956)
 25. *Protaphorura pseudocellata* (Naglitsch 1962)
 26. *Protaphorura pulvinata* (Gisin 1954)
 27. *Protaphorura quadriocellata* (Gisin 1943)
 28. *Protaphorura stachi* (Bagnall 1935)
 29. *Protaphorura subaequalis* (Bagnall 1937)
 30. *Protaphorura subarmata* (Gisin 1957)
 31. *Protaphorura sublata* (Gisin 1957)
 32. *Protaphorura subuliginata* (Gisin 1956)
 33. *Protaphorura s-vontoerneri* (Gisin 1957)
 34. *Protaphorura thalassophila* (Bagnall 1937)
 35. *Protaphorura tricampata* (Gisin 1956)
 36. *Protaphorura trinotata* (Gisin 1961)
 37. *Protaphorura tullbergi* (Bagnall 1935)
 38. *Protaphorura uliginata* (Gisin 1952)
 39. *Protaphorura waterstoni* (Bagnall 1937)
-

'species' of Onychiurinae could be recognised. Using the pseudocelli formula implies that the presence and position of each pseudocellus is under genetic control. However, the number and arrangement of pseudocelli within single populations, and even on different sides of the same individual, are variable

(Bödvarsson, 1970a; Lawrence, 1979; Pitkin, 1979, 1980; Pomorski 1986, 1990c), suggesting that they develop in 'fields'. It therefore seems unjustified to give many of these forms more than varietal status. For example, Table 5.1 is derived from the most recent checklists available for Britain. Kloet and Hincks (1964) and its update (Gough 1978) are certainly used if a quick answer is needed to the question 'how many species of *Protaphorura* are there in Britain?'. 'Officially' there are 39 but it is clear from the work of Pomorski (1990c) and others that there are probably far fewer biological species.

I am not suggesting that the morphotypes of *Protaphorura* described by Gisin and others do not exist, merely that there are differences of opinion on whether they should be given specific status. My own view is that most should be given the status of varieties of a much smaller number of species as the current practice of giving every minor variation a specific name gives a false view of the extent of biodiversity in Onychiurinae.

5.5 Conclusions and recommendations

Many people who would otherwise work on springtails are put off by the apparent complexity of the taxonomy. In principal, Collembola should be no more difficult to work on than other insects. Indeed, because springtails are preserved in alcohol or on slides instead of being glued to cards or pinned like wasps or beetles, they retain many features which would be lost in dry specimens. Nevertheless, there seems a reluctance on the part of collembolan taxonomists to write simple user-friendly keys for the novice.

Recently, however, there have been moves in the right direction. The key to Polish genera of springtails by Pomorski and Skarzynski (1992) is excellent and incorporates illustrated flow diagrams which are easy to use (e.g. Fig. 5.12). Fjellberg's (1994) key to the Collembola of the Norwegian Arctic Islands adopts a similar approach and is an excellent mixture of authoritative taxonomy and flow diagrams. Computer keys are only just beginning to be developed (for example the key to *Pseudosinella* by Christiansen *et al.* 1990), but it is clear that they will have an important role to play in the future.

Good taxonomy is vitally important in all branches of biology. It is very confusing when authors of papers give names to the species they are studying without citing the source. The following contentious names have been used by the authors in brackets without discussion of their validity:

Folsomia litseri (Dekkers *et al.* 1994)

Megalothorax incertus (Naeem *et al.* 1994, 1995)

Onychiurus procampatus (Bardgett *et al.* 1993a)

Onychiurus tricampatus (Hale 1966a, 1980)

Isotoma anglicana (Petersen 1995).

This may seem a trivial point but in these days of electronic indexing and literature searching, a stable internationally agreed standard terminology is essential.

Even if all possible characters (physical, ecological, behavioural, biochemical) are considered, it may still be impossible to decide on the boundaries of species with 100% certainty. Consequently, it would seem sensible to adopt a conservative line in describing new species if we are to avoid creating yet more synonymy for the collembolan taxonomists of the future to sort out.

I have presented the definition of the species concept as a problem. So let me end on a positive note with the following quote from O'Hara (1994).

In writing about species in the *Origin*, Darwin* often refers to them as 'permanent varieties' (1859, p. 475). I suggest that this is a particularly insightful phrase. Because evolutionary history is something we are still in the midst of, it will not always be possible for us to determine which varieties (which distinctive populations in nature) are temporary and which are permanent, and so our counts of species across space and through time will always have some measure of ambiguity in them that we cannot escape. If there is any consolation in this, it must be that the very existence of this ambiguity (the very fact that some organisms in nature cannot easily be grouped into species) is itself, as Darwin recognised, one of the most important pieces of evidence for the historical process we call evolution

* Darwin, C. (1859). *On the origin of species*. John Murray, London.

Interactions between Collembola and the abiotic environment

6.1 Introduction

Collembola have been on the Earth for more than 400 million years. During this time they have evolved to fill a huge variety of niches. Among the reasons for this success are small size, which enables them to colonise the gaps between soil particles, dead vegetation and other confined spaces, and physiological and behavioural adaptability. Tradition regards springtails as sedentary moisture-loving organisms which cannot survive dryness. However, this view is manifestly untrue, as will be shown in this chapter. There are springtails in deserts, in the coldest and driest parts of the earth, on the surfaces of most freshwater bodies and at the tops of the tallest trees. The only environments which Collembola have been unable to colonise are deep water and the open ocean.

Avoidance of abiotic extremes can be physiological or behavioural. The study of these strategies is often termed 'ecophysiology' and is important in understanding why particular species are restricted to certain environments (Bale 1987; Vannier 1983; Verhoef 1995). Physiological avoidance strategies include making the cuticle less permeable to water to reduce transpiration rates, or incorporating special chemicals in the blood to prevent freezing at sub zero temperatures. Behavioural avoidance strategies may be short term (e.g. climbing into a crevice during high tide to avoid drowning in littoral species) or long term (e.g. crawling to the deeper layers of the soil to avoid freezing in winter; Healey 1967). Some of the most highly adapted species may incorporate all of these strategies to enable them to persist in some of the most extreme environments on Earth.

Most springtails have a fairly cosmopolitan diet of fungi and decaying vegetation, or in surface and tree-climbing species, living vegetation, algae and pollen. Thus their distribution is most likely to be limited by the abiotic factors of temperature (Section 6.2), and availability of water (Section 6.3) and oxygen (Section 6.4), rather than presence of particular types of food. In this context, it is important to recognise that what limits the distribution of some populations is the time interval between limiting extremes in relation to the rate of dispersal of individuals, not necessarily the mean annual value. In other words, if the lower lethal temperature of a species is 0°C, then its long-term distribution will be limited to areas where this temperature is *never* reached, even though there may be a frost only once in every 30 years. Studies on the responses of organisms to rising temperatures have become pertinent with the advent of global warming (Danks 1992; Kennedy 1994).

6.2 Temperature

6.2.1 Introduction

The majority of species of Collembola live in regions where extremes of cold are not a major problem. Nevertheless, almost all studies on the effects of different temperatures on springtails have examined resistance to freezing. This imbalance in scientific activity is a reflection of the considerable resources put into Antarctic research. There are very few animals in Antarctica but Collembola form a higher proportion of the total fauna than in most other habitats on the Earth (Burn 1984a; Janetschek 1967; Peterson 1971; Salmon 1962a; Schaller 1992; Sømme 1985). It is ironic that one of the most inhospitable parts of our planet has supported the highest ratio of collembologists to species of springtail.

6.2.2 The 'thermobiological span'

Each species of collembolan has its own preferred temperature range between which it will settle if placed in a gradient (Babenko 1993; Fig. 6.1). The minimum

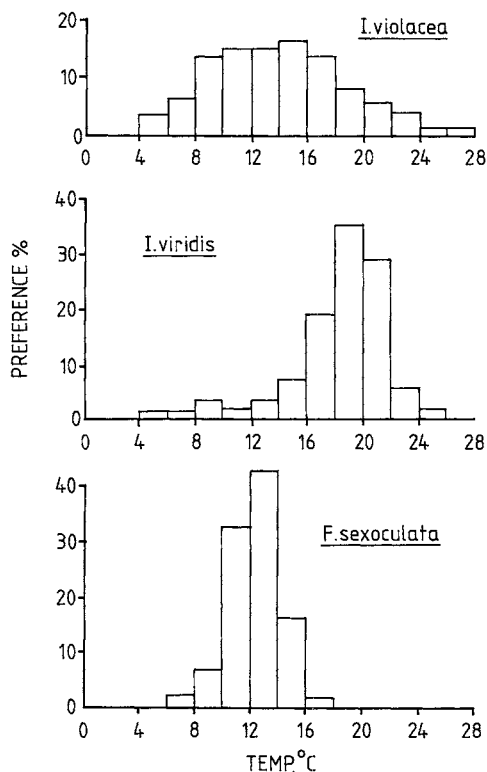


Fig. 6.1. Temperature preferences of *Isotoma violacea* (Isotomidae, 430 specimens), *I. viridis* (153 specimens) and *Folsomia sexoculata* (Isotomidae, 241 specimens) in a gradient of 20 cm in length (4°C at one end, 35°C at the other). The y axis shows the percentage of the total number of individuals which were found at a particular temperature, 3 h after introduction to the gradient. Redrawn after Babenko (1993) by kind permission of the author and the Russian Academy of Sciences.

lethal temperature is the *supercooling point* (SCP) at which the animal freezes. The SCP depends to a large extent on the physiological and chemical state of the animal and can therefore show considerable individual variation within a species (Rothery and Block 1992). Heat stupor occurs at the *thermostupor point* (TSP). This is the temperature at which the animal becomes suddenly motionless, but is a state from which it may recover with no long-term effects if returned quickly to a lower temperature.

The TSP is much less variable than the SCP and tends, not suprisingly, to be higher in springtails from warmer than cooler climates, and higher in epedaphic species than in euedaphic Collembola (Vannier 1987*b*). The *thermal death point* (TDP) may be higher than the TSP and is the temperature above which proteins denature, lipids melt and the animal dies (Thibaud 1975, 1977*a,b*; Vannier 1994). The absolute temperature range compatible with life is between the SCP and TSP and is called the *thermobiological span* (TBS). Vannier (1994) showed that for *Orchesella villosa*, the mean SCP was -9.4°C , the mean TSP was $+44.9^{\circ}\text{C}$, giving a mean TBS of 54.3°C .

It is no suprise that physiological and reproductive activities of springtails are related to temperature (Mertens *et al.* 1983). The relationship can be studied using the Arrhenius model which predicts a linear relationship between the logarithm of the egg development rate and the reciprocal of the temperature in degrees Kelvin (Van Straalen and Van Diepen 1995). The slope of the line equals $-H_A/R$, where R is the universal gas constant and H_A is the activation energy. The model assumes that the development rate is controlled by a single rate-limiting enzyme and that the reactants of the rate-limiting reaction have to surmount an energy barrier (the activation energy) to form the products. Thus, the Arrhenius activation energy may be estimated from linear regressions of logarithmically transformed rates versus reciprocal Kelvin temperatures.

Using this technique, Van Straalen (1994*a*) showed that for 38 species of Collembola, there was a negative correlation between development time at 15°C (d_{15}) and H_A (Fig. 6.2). Thus egg development times in epedaphic species such as *Orchesella cincta* tend to be more responsive to temperature than hemiedaphic species like *Tomocerus minor* (Van Straalen and Joosse 1985). In other words, the temperature response curve of *O. cincta* is steeper than *T. minor* and the former species is able to react much more rapidly to short-term temperature fluctuations than the latter. One consequence of this phenomenon is that epedaphic species such as *O. cincta* have more clearly defined size classes than euedaphic Collembola because the reproductive cycles of the former are synchronised closely with seasonal temperatures. Temperature fluctuations within the soil and in caves are less pronounced than at the surface. Thus euedaphic and cave-dwelling species tend to have overlapping generations since there is less need for them to use temperature changes to tune their development times to the seasons (Van Straalen 1994*a*).

6.2.3 Life at subzero temperatures

The physiology and behavioural mechanisms for survival at subzero temperatures are probably the most studied and best understood aspects of the biology of

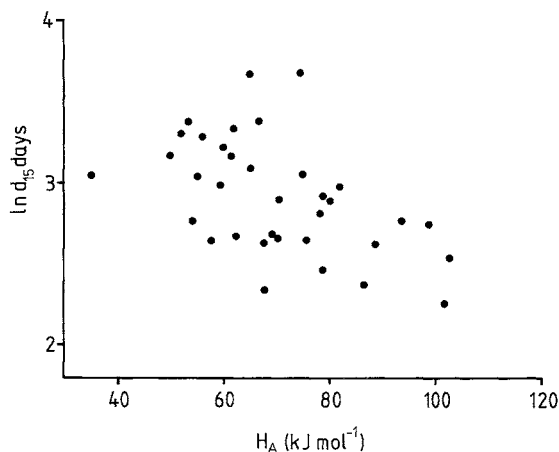


Fig. 6.2. Correlation between estimates of egg development times at 15°C (d_{15}) and activation enthalpies for a rate controlling enzyme (H_A) for 35 species of temperate Collembola. Redrawn after Van Straalen (1994a) by kind permission of the author and the Finnish Zoological and Botanical Publishing Board.

Collembola. Numerous excellent and comprehensive reviews have been published on the topic (Baust 1981; Block 1987, 1990, 1991; Cannon and Block 1988; Sømme 1981b, 1989, 1993). Thus I will give only a general overview in this Section.

Behavioural 'avoidance' of low temperatures is possible in regions without permafrost by searching out sheltered sites which are insulated from climatic extremes (Aitchison 1984; Brummer-Korvenkontio and Brummer-Korvenkontio 1980; Leinaas 1983a). For example, *Tomocerus minor* moves down the soil profile in response to a frost period without snow cover (Van der Woude and Verhoef 1986). It is also possible for Collembola to take advantage of brief periods of sunlight and warmth by 'basking' (Zettel and Zettel 1994c) or resuming feeding activity (Bale and Pullin 1991). Many species that live in cold climates are heavily pigmented which enables them to absorb more solar energy (Kopeszki 1988). Nevertheless, there are some species which remain active throughout the winter and this allows them to occupy a niche which might otherwise be filled by summer-active Collembola (Aitchison 1983; Itoh 1994a).

Collembola which live in habitats where subzero temperatures persist for a substantial part of the year have evolved physiological mechanisms to enable them to survive (Addison 1981; Leather 1995). Prolonged subzero temperatures increase the risk of tissue freezing. In terrestrial invertebrates, two main strategies of avoidance have evolved (Block 1994). First, avoidance of freezing by supercooling (Fig. 6.3) and second, tolerance of extracellular ice (Block 1990). In species employing the first strategy, called *freeze avoiding* by Bale (1993) (formerly known as 'freeze intolerant' species), freezing is invariably lethal and extensive supercooling (to -30°C and below) occurs through elimination or masking of potential ice nucleators in the body and accumulation of cryoprotective substances

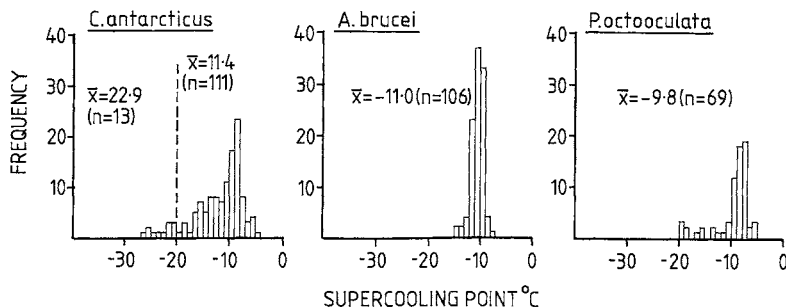


Fig. 6.3. Supercooling point distribution histograms for *Cryptopygus antarcticus*, *Archisotoma brucei* and *Parisotoma octooculata* (Isotomidae) at Signy Island during December-January of the 1981–82 austral summer. For *C. antarcticus*, the mean supercooling point is shown for a low group (left) and high group (right) with the division at -20°C . Redrawn after Block (1984b) by kind permission of the author and the British Antarctic Survey, Cambridge.

in the haemolymph such as sugars and polyhydric alcohols (Block 1979a, 1983, 1984b; Block and Sømme 1982; Block and Zettel 1980; Danks 1992; Leinaas and Sømme 1984; Meier *et al.* 1988; Sømme 1981a, 1986a; Zettel 1984b; Zettel *et al.* 1989). The second strategy, *freezing tolerance*, is uncommon in arthropods and involves freezing of the body tissues. This is protective and allows the frozen animal to survive temperatures well below the supercooling point. All Collembola studied so far are freeze avoiders; there are no freezing tolerant springtails (Block 1982c, 1985b).

Collembola can supercool to lower temperatures if they are slowly acclimated to a decreasing temperature regime rather than being suddenly cooled (Cannon 1983, 1986; Schenker 1983, 1984). They are also more resistant to freezing if conditions are dry (Block *et al.* 1994; Cannon *et al.* 1985; Sømme 1982), or their gut is empty (Chauvin and Vannier 1989). Particles of food in the digestive tract provide nucleation sites for ice crystals (Burn 1982; Sømme and Block 1982). Indeed at the onset of frost, *Orchesella cincta* evacuates its gut (Van der Woude 1987). There is also evidence that the degree of cold hardiness achieved is proportional to the availability of nitrogen in the food, at least in *O. cincta* (Ohlsson and Verhoef 1988). An increase in cold hardiness can also be achieved by exposing springtails to short photoperiods (8 h light, 16 h dark) which mimic the winter light regime (Van der Woude and Verhoef 1988; Von Allmen and Zettel 1984). Juvenile Collembola tend to be more cold hardy than adults of the same species (Zettel 1982a; Zettel and Von Allmen 1982).

Most experiments on cold hardiness have been conducted on *Cryptopygus antarcticus* (see Frontispiece). This species, which is abundant in Antarctica (Block 1980, 1982a; Burn 1984b), takes at least 2 years to mature so adults must be able to survive the very cold winter temperatures (Convey 1994). With the onset of winter, the animals accumulate cryoprotective substances and empty the gut. *C. antarcticus* can supercool to -30°C , but only if starved (Block 1981; Block *et al.* 1978). The supercooling point tends to be higher in the summer than the

winter (Lee and Baust 1981), and is consistently lower in *C. antarcticus* from the Antarctic than in populations of the same species from relatively warmer areas such as Signy Island (Block 1982b).

6.3 Water and salt balance

6.3.1 Introduction

Many species of Collembola live in intimate association with water (Thibaud and Massoud 1986a; Waltz and McCafferty 1979). Indeed, *Proisotoma roberti* from south west Greenland has been collected from bottom samples of shallow streams and may have a semi-aquatic lifestyle (Fjellberg 1991a). Some Collembola are vulnerable to drowning when their habitat floods (Mertens *et al.* 1983). This may be an occasional phenomenon in euedaphic species when the soil becomes water-logged after heavy rain, or a regular event in littoral species such as *Anurida maritima* which live in the tidal zone (Joosse 1966). Even springtails which live on trees and can escape flooding must have water-resistant eggs if these are laid in the soil (Tamm 1984, 1986a).

At the opposite extreme, some Collembola have to tolerate dry conditions in deserts (Greenslade 1981, 1982a; Greenslade and Greenslade 1984; Loring *et al.* 1988; Thibaud and Massoud 1988) or polar regions (Block *et al.* 1990; Hodgkinson *et al.* 1994a; Worland and Block 1986) where there may be little or no free water for months on end.

The concept of 'water accessibility' is crucial for understanding the moisture relations of Collembola (Ellis 1974a; Thibaud and Vannier 1969; Vannier 1971, 1978a, 1983, 1987a). Even if a soil can be shown to contain water (i.e. it loses weight when dried in an oven at 70°C), it may be unavailable for euedaphic Collembola living in the spaces between clumps of soil particles. Soil was the route through which invertebrates colonised terrestrial environments. Collembola provide a clear example of a range of species from those which live permanently in moist soil and have few mechanisms to restrict water loss, through to epedaphic species that climb trees and are highly resistant to desiccation.

6.3.2 Sites of water and ionic exchange with the environment

The main site of water and salt exchange in Collembola is the apical surface of the ventral tube (Sedlag 1952; Fig. 6.4). The tube is formed from a pair of abdominal vesicles on the first segment of the abdomen which are derived from appendages. The external surface bears mechanoreceptive bristles (Eisenbeis 1976a) and chemosensory sensilla which are sensitive to water, salts, and extremes of pH (Eisenbeis 1976b; Jaegar and Eisenbeis 1984).

The apical region of each ventral tube hemisphere is covered with a very thin cuticular layer beneath which are a small number of transporting cells (typically 20 in *Tomocerus* and *Orchesella*) that are rich in mitochondria. Basally, the cells form prolonged processes which extend through the whole ventral tube to the abdomen (Eisenbeis 1974). In *Folsomia candida*, the transporting cells exhibit

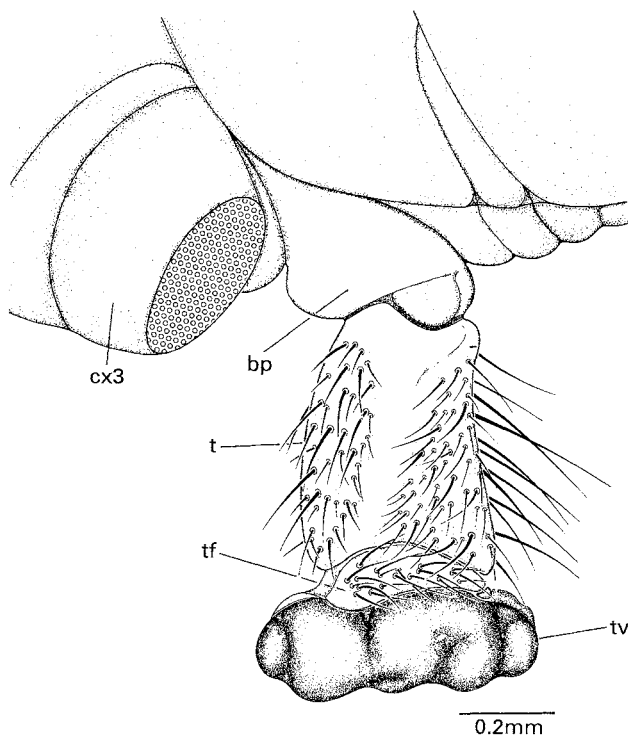


Fig. 6.4. Semischematic diagram of the ventral tube of *Tomocerus* sp. (Tomoceridae). bp, basal plate; cx3, coxa of leg 3 (omitted); t, tube cylinder; tf, tube valves; tv, tube vesicles. Reproduced from Eisenbeis (1974) by kind permission of the author and the *European Journal of Cell Biology*.

considerable changes in their ultrastructure when the animals are exposed to solutions of sodium chloride. Noble-Nesbitt (1963*b*) showed that in *Podura aquatica*, the main site of uptake of radioactive sodium (^{24}Na) is via the ventral tube. The ultrastructure of the ventral tube has also been described in *Tetradontophora biela-nensis* by Rosciszewska and Ksiazkiewicz (1981).

The ventral tube is connected via a groove called the *linea ventralis* (see Fig. 4.13) to the openings of the nephridial organs or 'kidneys' (Rusek 1987*b*; Verhoef *et al.* 1979, 1983; Fig. 4.12; Section 4.3.3). Urine from the kidneys passes by capillary action along the groove to the ventral tube.

In experiments on *Orchesella cincta* and *Tomocerus minor*, Verhoef (1981) and Verhoef and Prast (1989) could find no evidence for osmoregulation. The osmotic pressure of these two species varies between about 300–400 mOsm l^{-1} which falls within the range typical of most insects (300–500 mOsm l^{-1}). The urine of fully hydrated animals is hypoosmotic with the haemolymph, however after dehydration, the urine becomes isoosmotic. *O. cincta* reacts much more rapidly to changes in external moisture than *T. minor* reflecting the more epedaphic lifestyle of the former (Vannier and Verhoef 1978; Verhoef and Prast 1989; Verhoef and

Witteveen 1980). Indeed, lost water can be replaced 8–10 times faster in *O. cincta* than in *T. minor* (Eisenbeis 1982; Verhoef 1981). The osmolarity of the haemolymph reaches much higher values in Collembola in saline environments (Section 6.3.5).

The ventral tube is permeable to small organic molecules. Their rates of uptake are inversely proportional to molecular mass, especially in the range 100–200 (Schreiber and Eisenbeis 1985). Nevertheless, absorption by the ventral tube is not important for nutrition. Calculations by Schreiber and Eisenbeis (1985) have shown that absorbed glucose could only provide 0.013% of the amount the animals need for respiration.

Water may also be lost across the body surface but the rate is quite low in species from dry environments (Harrisson *et al.* 1990, 1991; Vannier 1972, 1973*a,c*, 1976). It is difficult to attribute all water lost to cuticular transpiration as some liquid probably evaporates from the vesicles of the ventral tube. The potential for water loss is greatest during moulting when the animals need to be fully hydrated to provide sufficient pressure to split the old exoskeleton and expand the new one (Vannier 1973*b*; Verhoef 1981). Water can be replenished by drinking. In *Podura aquatica* this is an extremely important mechanism of rehydration when the haemolymph pressure is too low for eversion of the ventral tube vesicles (Noble-Nesbitt 1963*b*). In *Sminthurus viridis*, droplets of water can be conveyed from the hairs of the body to the mouth via the extremely long ventral tube (Davies 1928*b*) which is covered in small papillae (Eisenbeis and Wichard 1987).

Thus the water and salt content of a springtail is influenced by the amount and osmolarity of the urine produced by the kidneys, the amounts of water and salts absorbed from, or lost to, the external environment via the ventral tube, body cuticle and gut, and the volume of water taken in through the mouth (Eisenbeis and Wichard 1975*a,b*).

6.3.3 Resistance to flooding

Collembola can avoid becoming waterlogged by behavioural means. Thus if the bases of trees become too wet for *Allacma fusca* and *Orchesella flavescens*, they climb up the trunk to drier bark (Bauer 1979). Individuals of the marine littoral collembolan *Anurida maritima* clump together in small 'nests' which are filled with air during inundation at high tide (Joosse 1966; Witteveen *et al.* 1988).

The structure of the cuticle is also important in preventing waterlogging. *Anurida maritima* possesses a plastron supported by minor tubercles which is resistant to wetting by pressure and surfactants (King *et al.* 1990; Fig. 4.9). Thus this species, and probably many soil dwellers that are subject to periodic flooding (Zinkler and Rüssbeck 1986), retain a layer of air over the body across which they continue to respire, even when totally submerged. Eggs may also be adapted for prolonged submergence in water (Tamm 1984, 1986*a*; Zeh *et al.* 1989).

Most springtails will float on the surface of a liquid, at least for a short time, and there are several Collembola such as *Podura aquatica* which are adapted for life on the water film (Noble-Nesbitt 1963*a*).

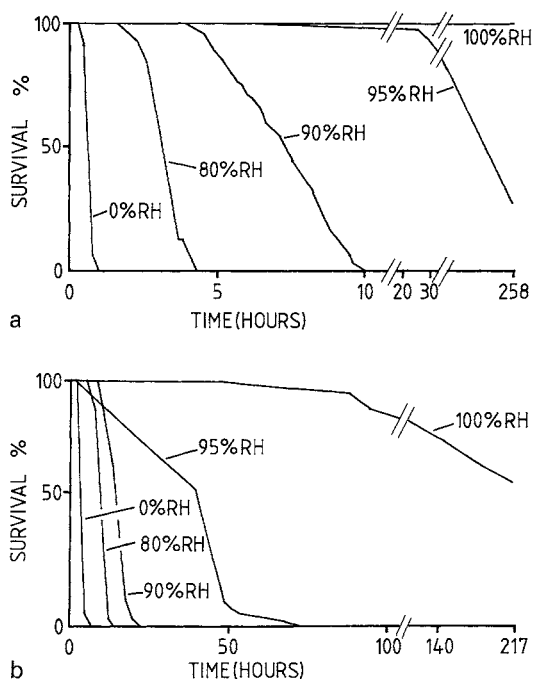


Fig. 6.5. Mortality of '*Onychiurus justus*' (Onychiuridae) at five relative humidities at (a) 10.0°C and (b) 26.6°C (100 individuals in each case). Redrawn after Snider and Butcher (1972) by kind permission of the authors.

6.3.4 Resistance to desiccation

As the temperature increases, the survival times of Collembola at specific relative humidities declines (Snider and Butcher 1972; Fig. 6.5). The different adaptations of Collembola to avoid water deficits exhibit convergences with those developed to resist low temperature (Poinsot-Balaguer and Barra 1991; Snider and Butcher 1972; Sømme 1994; Vannier 1979a). Collembola are apparently unable to regulate their water content at a specific level in a saturation deficit, but they have evolved several ways to reduce the rate of water loss. Their rate of desiccation can be regulated by behavioural or physiological means, or by a combination of the two (Poinsot-Balaguer 1990). Unless they are in a desiccation-resistant phase (see below), springtails must return periodically to a place where water is available to allow them to rehydrate (Loring 1981).

Several species of Collembola are found in ecosystems which are extremely dry for at least part of the year (Suhardjono and Greenslade 1994). Greenslade (1981) recognised six strategies for survival in arid areas:

- morphological and physiological adaptations that give tolerance of high temperature and saturation deficits
- behaviour that minimises the risk of desiccation

- inactive desiccation-resistant juvenile or adult stages that are rapidly reactivated by moisture (anhydrobiosis and ecomorphosis)
- 'dormant' eggs that hatch in moist conditions
- distribution restricted to moist habitats
- very short life history.

These strategies have been adopted by a wide range of Collembola and some examples are given below.

- The ornamentation of the cuticle of *Anurida maritima* is arranged in such a way that a very thin layer of water-saturated air is trapped against the body. This slows down water loss and allows the species to forage in the upper littoral zone where it is dry. *Anuridella marina*, which does not possess such a layer has a higher transpiration rate and is confined to more humid habitats near the sea (King *et al.* 1990).
- Behavioural methods to reduce water loss include aggregation (Joosse and Groen 1970), or the building of a chamber from soil and faecal particles in which the relative humidity is maintained at a high level during moulting (Massoud *et al.* 1968; Poinot 1966; Pomorski and Weichsel 1993).
- Many springtails stop feeding in response to low relative humidity and go into a 'dormant' or quiescent state (Testerink 1983; Verhoef and Li 1983). In some species, this is called the *ecomorphic state* (see Section 8.6 for further details). Collembola in this condition exhibit morphological features that are not present in normal adults (Raynal 1974). An extreme form of ecomorphosis is *anhydrobiosis*. In some species of *Folsomides*, this is manifested by a lowering of metabolic activity (Belagnaoui and Barra 1988a), a reduction in water and glycogen content (Belagnaoui and Barra 1988b), and filling of transcuticular channels with a hydrophilic substance. In this somewhat shrivelled state, the animals are able to survive dehydrating conditions and temperatures that kill those not in the anhydrobiotic condition (Belagnaoui and Barra 1989). Indeed, anhydrobiotic specimens of *Folsomides angularis* will rehydrate with no apparent ill effects after being cooled to -180°C (Poinot-Balaguer and Barra 1983). When moisture returns, the material in the cuticular channels disappears and the springtail becomes active again (Barra and Poinot-Balaguer 1977, 1983; Barra *et al.* 1989).
- In Provence, France, the majority of species of Collembola pass the dry summer as a resistant egg stage (Poinot 1971). Greenslade and Greenslade (1973) cite several examples of species of Collembola which live out dry periods as drought-resistant eggs.
- The reactions of Collembola to saturation deficits are related to preferences in their natural habitats (Joosse and Groen 1970; Vannier 1977a,b). Species that live in permanently moist habitats such as wet caves (Thibaud and Vannier 1980; Vannier and Thibaud 1978) or decaying wood in rain forests (Vannier and Najt 1991) have little need to regulate water loss in comparison to those

which spend most of their time under dry conditions (Vannier 1974*a,b*, 1975*b*). For example, in conditions of low humidity, the soil-dwelling species *Protaphorura fimata* has a water transpiration rate of $800 \mu\text{g cm}^{-2} \text{h}^{-1} \text{mmHg}^{-1}$ whereas *Seira domestica* (which is often found in centrally heated houses, including my own) dehydrates very slowly with a transpiration rate of only $3 \mu\text{g cm}^{-2} \text{h}^{-1} \text{mmHg}^{-1}$ (Verhoef and Prast 1989). Harrison *et al.* (1990) reviewed rates of water loss in 16 species of Collembola.

- Bauer (1993) and Bauer and Christian (1993) studied the collembolan community of large granite boulders in Austria. The microclimates on different parts of the boulders are extremely variable and the habitat preferences of the different species could be related to their resistance to drying (Fig. 6.6). Thus *Protaphorura armata*, which has poor drought resistance, lives in stable plant cushions connected to the surrounding soil by strips of moss. *Pseudisotoma sensibilis*, which has intermediate drought resistance, prefers cushions not far above the ground and frequently migrates between rock and soil. The highly drought-resistant species *Xenylla boernerii*, dominates the tops of the boulders and is able to cross dry rock surfaces between the highly exposed moss cushions.
- A population may persist in a region where rainfall is infrequent by having a very rapid life cycle. The juvenile and adult stages, which are the most vulnerable to desiccation, are passed through very quickly and most of the life cycle during the year is taken up by a drought-resistant egg stage. Greenslade (1981) quoted the example of a species of *Sphaeridia* (Sminthuridinae) from the arid Koonamore regions of Australia, in which the complete life cycle from egg to egg takes only one week in the laboratory.

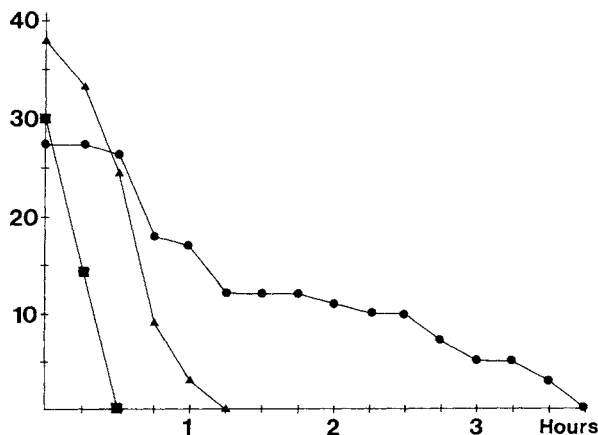


Fig. 6.6. Drought resistance at 25°C (55% relative humidity) of *Protaphorura armata* (Onychiuridae, squares), *Pseudisotoma sensibilis* (Isotomidae, triangles) and *Xenylla boernerii* (Hypogastruridae, circles). Each point represents the number of individuals not affected by drought-coma. Reproduced from Bauer and Christian (1993) by kind permission of the authors and Gustav Fischer.

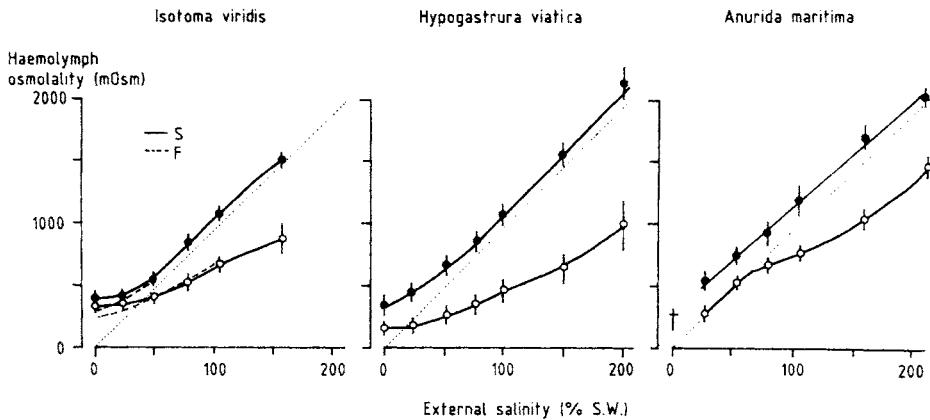


Fig. 6.7. Total osmotic (closed circles) and ionic (open circles) concentration (mOsm kg^{-1}) of the haemolymph of *Isotoma viridis* (Isotomidae), *Hypogastrura viatica* (Hypogastruridae) and *Anurida maritima* (Neonuridae) after acclimation to a series of soil water salinities. Mean \pm standard deviation ($N = 6$). F, inland population; S, salt marsh population. The dotted lines indicate lines of equality. Reproduced from Witteveen *et al.* (1987) by kind permission of the authors and Elsevier Science Ltd.

6.3.5 Tolerance of high salinity

Marine littoral and salt marsh habitats are harsh environments where Collembola may be exposed to considerable osmotic stress (Cheng and Frank 1993; Joosse 1976; Witteveen 1988; Witteveen and Joosse 1982, 1987, 1988). Witteveen *et al.* (1987) performed an interesting study in which they compared osmotic and ionic regulation in the grassland species *Isotoma viridis*, the salt marsh *Hypogastrura viatica* and the intertidal *Anurida maritima* (Fig. 6.7). The results of their experiments are summarised below.

When concentrations of salt in the soil water are low ($<50\%$ seawater), *I. viridis* and *H. viatica* hyper-regulate the osmotic and ionic concentration of the haemolymph. At higher external salt concentrations they behave as osmoconformers. *A. maritima* has lost the ability to hyper-regulate and is an osmoconformer suffering high mortality at low salinities. *A. maritima* is an example of a terrestrial arthropod which has become physiologically tied to a saline environment. In freshwater conditions, an inland population of *I. viridis* maintained a lower osmotic and ionic concentration than a population of the same species from a salt marsh. This is an interesting example of an early stage in possible 'physiological speciation' although it is not known to what extent the two races of *I. viridis* would remain reproductively isolated if mixed together.

6.4 Gaseous exchange and metabolism

Collembola are small animals with a high surface area to volume ratio. Gaseous exchange takes place across the cuticle of the body and the moist surface of the

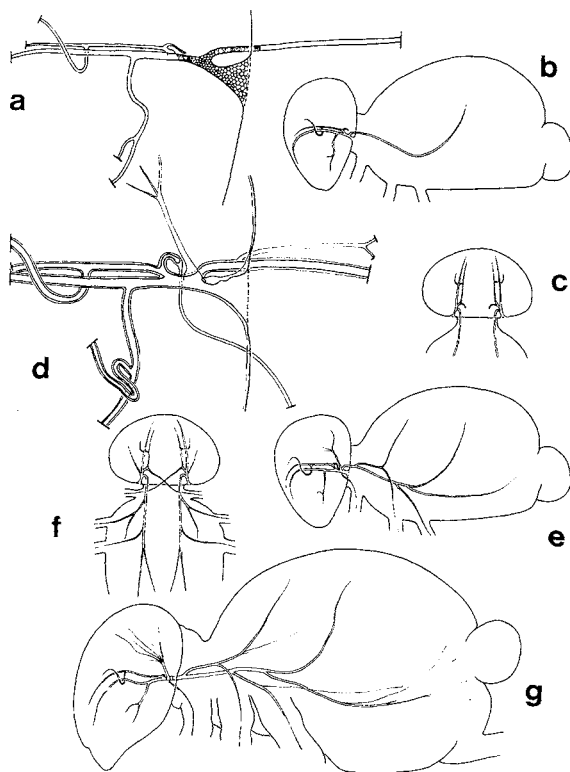


Fig. 6.8. Development of the tracheal system of *Allacma fusca* (Sminthuridae). (a–c) Early first instar individual; (d–f) late first instar individual; (g) third instar individual. Reproduced from Betsch and Vannier (1977) by kind permission of the authors and Blackwell Wissenschafts-Verlag, Berlin.

ventral tube (and in a few cases via tracheae). However, the proportion of the total accounted for by the ventral tube has not been ascertained.

In most species, the cuticle is not a significant barrier to the diffusion of gases between the body tissues and the atmosphere. Nevertheless, species in the Family Actaletidae and Subfamily Sminthurinae possess tracheae which increase the surface area available for gaseous exchange (Betsch and Vannier 1977; Davies 1927; Fig. 6.8). If one accepts that these taxa are 'advanced', then tracheae must have arisen independently in Actaletidae and Sminthurinae from atracheate ancestors. The fine structure of the tracheae is identical with that of other insects and therefore provides an excellent example of convergent evolution (Xué *et al.* 1994). The tracheae open to the atmosphere through a pair of spiracular openings on the head near the neck region, the diameter of which cannot be altered (Eisenbeis and Wichard 1987). The only other Collembola in which possible accessory respiratory structures have been found are members of the Subfamily Spiniothecinae. These unusual sminthurids have a pair of bulbous neck organs which surround the posterior of the head rather like an orthopaedic neck brace (Greenslade 1982*b*).

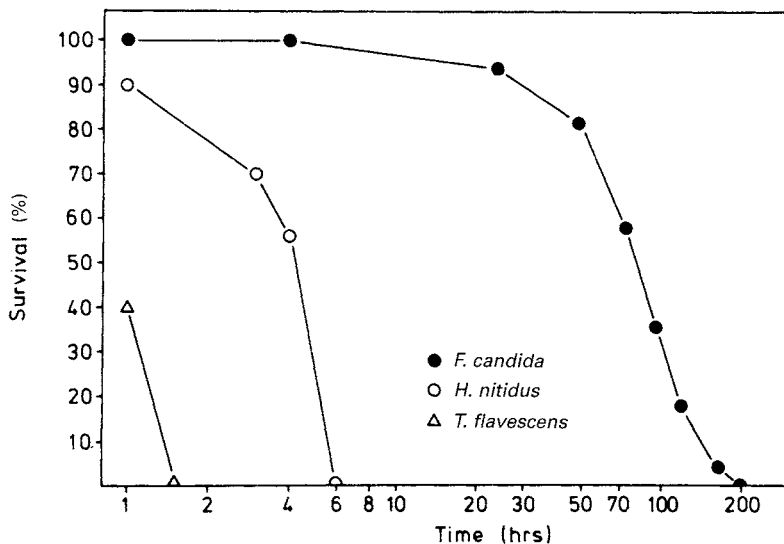


Fig. 6.9. Survival rates of *Folsomia candida* (Isotomidae), *Heteromurus nitidus* (Entomobryidae) and *Pogonognathellus* (= *Tomocerus*) *flavescens* (Tomoceridae) stored in nitrogen at 18°C ($N = 15$). Reproduced from Zinkler and Rüssbeck (1986) by kind permission of the authors and the University of Siena.

When soil is flooded, small bubbles of air often persist between the particles into which oxygen diffuses from the surrounding water. Although the oxygen concentration in these pockets of air may be lower than normal, euedaphic species such as *Folsomia candida* can remain within them and continue to be active down to partial pressures of only 8 mmHg equivalent to only 1% oxygen (Zinkler and Rüssbeck 1986). Indeed, *F. candida* had a 40% survival rate after four days in pure nitrogen whereas two hemiedaphic species were all dead within a few hours (Fig. 6.9). Some species carry around their own 'air pocket' by trapping a thin layer of air at the surface of the cuticle using a plastron into which oxygen diffuses from the surrounding water (see Fig. 4.9).

Species which become enclosed in pockets of air in water or ice into which oxygen cannot diffuse, must be able to survive for long periods under completely anaerobic conditions (Leinaas and Sømme 1984; Sømme 1993). For example, *Cryptopygus antarcticus* had a 30% survival rate after 30 days in pure nitrogen (Sømme and Block 1982).

Respiration rates are determined from rates of oxygen consumption, or carbon dioxide production (Sustr and Simek 1994). However, it should be remembered that oxygen consumption is an indirect method of determining respiration and that total energy consumption is the sum of metabolism, growth and egg production (Testerink 1982). Due to the small size of Collembola, oxygen consumption rates are usually measured in a cartesian diver (Block and Tilbrook 1975, 1977, 1978). Respiration tends to be lower in animals that are starved, moulting or undergoing

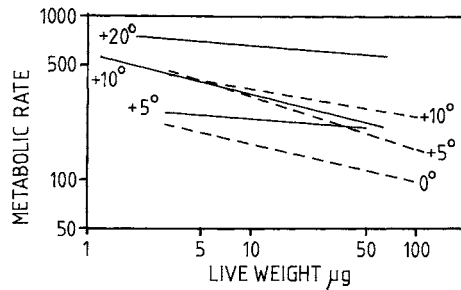


Fig. 6.10. Metabolic rate ($\mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$) as a function of live weight for *Cryptopygus antarcticus* (Isotomidae) at South Georgia at 5, 10, and 20°C (solid lines) and Signy Island at 0, 5, and 10°C (dashed lines). Data are plotted on a double \log_{10} scale and the linear regression line is shown for each temperature. Redrawn from Block and Tilbrook (1978) by kind permission of the authors and *Oikos* Editorial Board, Lund, Sweden.

periods of quiescence during frost or summer drought (Van der Woude and Joosse 1988; Zettel 1982*b*). It is also affected greatly by the humidity and temperature of the air. Thus, conditions have to be tightly controlled to allow comparison between experiments conducted in different laboratories (Verdier and Vannier 1984).

Epedaphic springtails have higher oxygen consumption rates than euedaphic species with hemiedaphic species somewhere inbetween (Petersen 1980; Vannier and Verdier 1981). These differences are related to the relatively greater activity of epedaphic species which are continually on the move avoiding predators and searching for high quality food (Petersen 1980). Polar species such as *Cryptopygus antarcticus* and *Parisotoma octooculata* also tend to have higher metabolic rates than temperate species of similar size and this may improve their cold hardiness (Block 1979*b*; Tilbrook and Block 1972).

Oxygen consumption increases with temperature. This relationship is often expressed as the Q_{10} , which is the increase accompanying a temperature rise of 10°C. The Q_{10} of *Protaphorura meridiata*, for example is, 2.45 (Argyropoulou and Stamou 1993). Petersen (1981) reported mean values of Q_{10} between 1.9 and 3.4 in a range of species of temperate Collembola and this agrees with most other values for arthropods (with the exception of *Pogonognathellus flavescens* which inexplicably has a Q_{10} of 5.2). Juveniles tend to have higher consumption rates of oxygen than adults of the same species (Fig. 6.10).

Interactions between Collembola and the biotic environment

7.1 Introduction

Collembola consume a wide variety of food materials, especially fungal hyphae (Section 7.2). Recent experiments on euedaphic species suggest that soil springtails are very important in either stimulating or suppressing microbial symbionts around plant roots (Klironomos and Kendrick 1995*b*; Lussenhop 1993, 1996). Collembola have numerous predators and parasites, they interact among themselves, and occur as 'guests' in the nests of eusocial insects such as ants and termites (Section 7.3). A major beneficial effect of collembolan feeding activity is the promotion of decomposition processes in soils (Rusek 1975*a*). This occurs through direct feeding on dead vegetation and fungal hyphae, and indirect stimulation of microbes involved in decomposition (Section 7.4).

A few species of springtail are occasional pests of food crops (Section 7.5). However, this situation may arise through accidental introduction by humans. In Australia, *Sminthurus viridis* is a pest of clover and is known as the 'Lucerne flea'. *S. viridis* is native to the Northern Hemisphere. In Australia, there are too few natural enemies to maintain the populations below pest levels of abundance.

7.2 Feeding behaviour

7.2.1 Assimilation efficiencies and starvation

The assimilation efficiency of feeding (AE%) can be calculated from the formula $AE = ((D - F)/D) \times 100$ where D = dry weight of food consumed and F = dry weight of faeces voided. The AE of specific substances can be calculated in a similar way by comparing concentrations in faeces and food. This approach allows comparisons to be made between the AE in different individuals of the same species on different diets. Thus Burn (1984*b*) showed that the AE of juvenile *Cryptopygus antarcticus* feeding on algae was 46% whereas for adults it was only 19%; the values when feeding on moss peat were 7% and 10% respectively.

These differences broadly reflect nutritional quality. Not surprisingly, consumption of better quality food leads to greater fecundity and growth rates (Snider 1971; Von Allmen and Zettel 1983; Whipps 1993; Zettel 1982*b*). However, there are large deviations in the AE of individual components of the diet. For example, sugars will have a much higher AE (probably approaching 100%) than celluloses of plant cell walls which are highly resistant to digestion (Saur and Ponge 1988). Furthermore, microorganisms adhering to the surfaces of ingested plant material

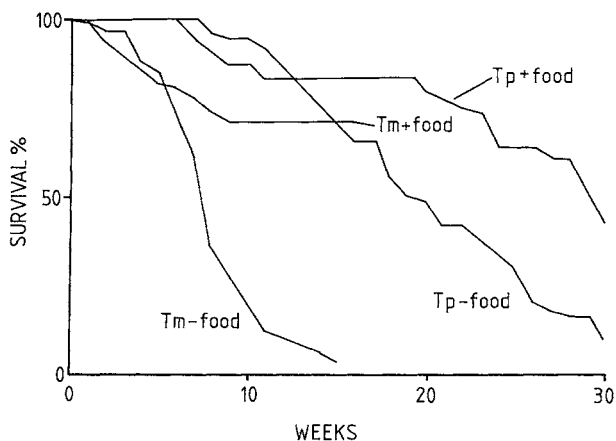


Fig. 7.1. Mortality of *Tomocerous problematicus* (Tp, Tomoceridae) and *Tomocerous minor* (Tm) on a clay substrate with or without food. Number at start of experiment; Tm with food = 109, Tm without food = 119; Tp with food = 50, Tp without food = 50. Redrawn from Christiansen (1970b) by kind permission of the author.

are digested with greater efficiency than the fragments of vegetation. The latter may be excreted in the faeces relatively unchanged. The total AE thus gives a relatively crude indication of digestive efficiency in Collembola.

Laboratory experiments in which springtails are kept in optimal conditions may also overestimate feeding and assimilation rates in comparison to more rigorous field conditions (Petersen 1975). Thus it is difficult to give a 'typical' AE for Collembola. The value will lie somewhere within the range for all soil arthropods of 1–65% (Petersen and Luxton 1982) depending on the physiology of the animal, the type of food being consumed, climatic conditions, and the substance being measured (Wolters 1985).

Active Collembola (i.e. those not in an ecomorphic state; Section 8.6) can survive without food by drawing on their reserves of lipids and glycogen (Testerink 1981; Verhoef and Li 1983). Tolerance of starvation is a characteristic feature of cave species. The record appears to be held by an individual of *Bonetogastrura balazuci* which survived with no food for 560 days on a mixture of moist clay from its cave and plaster of Paris (Thibaud 1981). In experiments comparing starved specimens of the hemiedaphic *Tomocerous minor* with the cave-dwelling *Tomocerous problematicus*, Christiansen (1970b) showed that the survival rates of the latter species were about twice those of the former (Fig. 7.1). The Collembola were maintained on a clay substrate from which they may have been able to graze chemosynthetic bacteria. Nevertheless, this source of nutrition was insufficient for long-term survival and successful reproduction.

7.2.2 Methods of assessing feeding activity and choice of foods

One of the principal methods of avoiding niche overlap in species which live in physically similar niches is dietary specialisation. Thus the study of the natural

diets of springtails is important for an understanding of their basic ecology, as well as their influence on microbial populations and role in decomposition (Vegter 1983). Many attempts have been made to elucidate the natural diets of Collembola but all are fraught with problems. It may be easy to demonstrate that a particular species will show a preference for a specific type of food in the laboratory (Thiele and Larink 1990; Van Amelsvoort and Usher 1989b), but it is more difficult to prove that it will be chosen under field conditions (Matic and Koledin 1985; Petersen 1971a; Verhoef *et al.* 1988).

One way around this problem is to collect springtails from the wild and examine their gut contents or faecal pellets (Anderson and Healey 1972; Chen *et al.* 1996; Hodkinson *et al.* 1994b; McMillan 1975; Fig. 7.2). However, the material in the lumen of the digestive tract may be difficult to recognise after it has been 'chewed' by the mandibles and attacked by digestive enzymes (Massoud and Najt 1976). Specific identification of fungi is extremely hard although the species of plant from which pollen grains were derived can usually be recognised. Just because a springtail has ingested something does not imply that it will derive any nutritional benefit from it. It may have fed on it accidentally. Material found in the faeces such as viable algal or bacterial cells or fungal spores has obviously been 'rejected' in the sense that it has not been digested (Gomez *et al.* 1990; Poole 1959; Vannier 1979b).

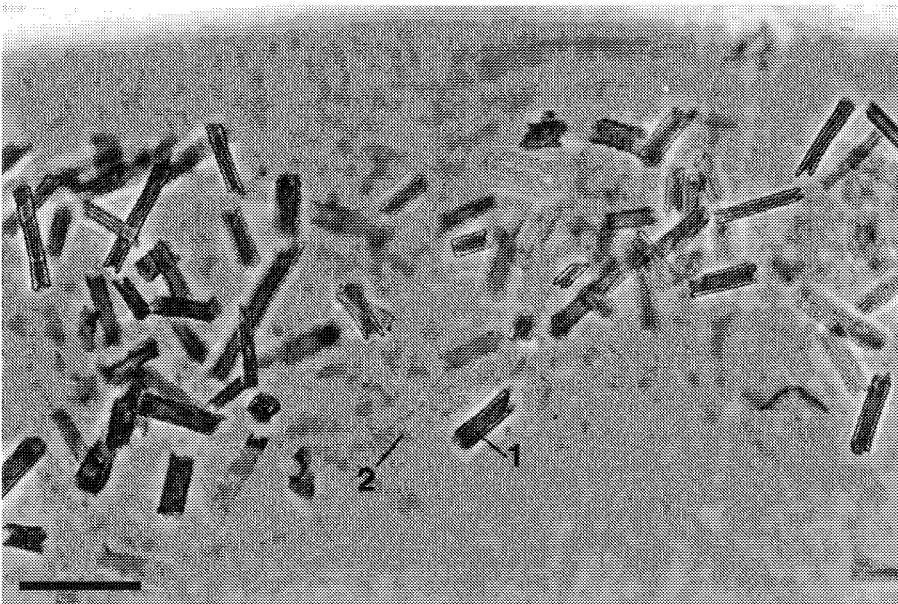


Fig. 7.2. Light micrograph of hyphae of two mycorrhizal fungi, *Cenococcum geophilum* (melanized walls, 1) and *Hyphodontia* sp. (hyaline hyphae, 2) in the gut of *Pseudosinella terricola* (Entomobryidae). Only the hyaline hyphae were being digested. Scale bar = 20 μ m. Reproduced from Ponge (1991a) by kind permission of the author and Elsevier Science.

Until recent years, the main conclusion of this type of work has been that in most habitats, the majority of euedaphic and hemiedaphic Collembola are generalists and seem to ingest whatever fungi, lichens, decomposing vegetation or detritus is available (Al-Safadi 1988; Block 1985a; Bödvarsson 1970b; Gilmore and Raffensperger 1970; Leinaas and Fjellberg 1985; Lupetti *et al.* 1989; Muraleedharan and Prabhoo 1978; Poole 1959; Schultz 1991; Takeda and Ichimura 1983). In addition to these food sources, epedaphic species may feed on living vegetation, pollen, and algae which they graze from the bark of trees (Bauer 1979; Kato 1995; Kevan and Kevan 1970; Kowal and Crossley 1971; Marshall 1978; Petersen 1971a; Tosi *et al.* 1977). In the words of McMillan and Healey (1971), 'it is difficult to avoid the conclusion that [Collembola] feed unselectively and that their gut contents represent a random selection of the components of their environment'. Indeed the opportunistic nature of the feeding behaviour of many species of Collembola may be one reason for their success.

However, other experiments and observations have shown that some species of Collembola show definite preferences for certain types of food. Even species which are taxonomically close may choose to eat different diets in the field (Chen *et al.* 1995, 1996). There is a tendency for fungal hyphae to be preferred above other food types (Broady 1979; Knight and Angel 1967). Collembola which feed on leaf litter prefer to ingest material in an advanced stage of decomposition from which secondary defensive chemicals have been leached, and on which there is a well-developed microbial flora (Sadaka and Poinso-Balaguer 1987, 1989; Sadaka *et al.* 1989; Scholle *et al.* 1995). They may also ingest the faecal pellets of other soil animals (Ponge 1991a). Indeed, *Tomocerus vulgaris* dies within a month if maintained elm leaves which have been sterilised (Sharma 1967). Collembola also prefer to feed on the more delicate parts of a plant such as new shoots, fine rootlets, or mycorrhizae, than mature leaves or roots (Hurej *et al.* 1992; Ulber 1980).

The best evidence for selective feeding is provided by laboratory experiments on fungal feeding which are reviewed below (Section 7.2.4).

7.2.3 Carnivorous Collembola

Most Collembola consume material derived from animals from time to time. This may be accidental; for example, when tiny fungivorous nematodes are ingested along with the fungus on which the springtail is feeding (Walter 1987). However, Gilmore (1970) has suggested that Collembola feed deliberately on plant pathogenic nematodes and may be beneficial in their control. Conversely, Gilmore and Potter (1993) showed in laboratory experiments that both *Folsomia candida* and *Sinella coeca* consumed large numbers of entomopathogenic nematodes which are used as biocontrol agents for larvae of wax moths (*Galleria mellonella*) and Japanese beetle (*Popillia japonica*); in this situation the Collembola could be regarded as a nuisance.

Springtails are often facultative feeders on dead animals and in addition to direct consumption, may graze fungal hyphae growing on the corpse (Payne *et al.*

1968). Other Collembola may consume fragments of animal material, including other springtails (Tosi 1977). Nayrolles (1990c) found fragments of moths and Collembola in the gut of species of *Arrhopalites* (Katianninae) in Thai caves where decaying vegetation is scarce. Dasgupta and Dasgupta (1990) found Collembola feeding on wounds in the skin of captive frogs and newts.

There are some springtails which are definitely carnivorous. Species of *Friezea* prey on the eggs of other Collembola from which they remove the contents with their piercing mouthparts (Petersen 1971a); they also consume tardigrades and rotifers (Palacios-Vargas and Acosta 1994; Usher and Booth 1984). In his redescription of *Cephalotoma grandiceps*, Cassagnau (1972a) suggested that the asymmetrical mandibles of this Arctic species were adapted for active predation. The gut contained fragments of other Collembola which supported his suggestion. It would be fascinating to collect live specimens of *C. grandiceps* and observe its predatory behaviour in the laboratory.

7.2.4 Fungal feeding

Why do springtails eat fungi? The most obvious reason is that the hyphae provide rich sources of nutrients which have been released from plant material by fungal digestive enzymes which Collembola are not able to produce themselves (Bakonyi *et al.* 1995). Indeed, fungi probably provided the main source of food for the early arthropod colonisers of the land (Price 1988). Several studies have demonstrated the importance of fungi in collembolan nutrition (e.g. Draheim and Larink 1995; Klironomos and Kendrick 1995a; Mills and Sinha 1971; Moore *et al.* 1987; Ponge and Charpentié 1981; Visser *et al.* 1987). Collembola graze fungi from a wide variety of sources including the surfaces of decaying leaves, faecal pellets and soil particles (Anderson and Ineson 1984; Bardgett *et al.* 1993b,c; Ponge 1991b). Many species are found in association with toadstools (Palacios-Vargas and Gomez 1991) and bracket fungi (Hingley 1971). Hypogastrurids are familiar pests of commercial mushroom houses.

Collembola may be beneficial in consuming plant-pathogenic fungi (Hiol *et al.* 1994; Nakamura *et al.* 1991a,b; Williets *et al.* 1989). For example, Nakamura *et al.* (1992) showed that the grazing activities of *Sinella curviseta* (Entomobryinae) suppressed the fungus *Fusarium oxysporum* f. *cucumerinum* which causes wilting disease of cucumbers. Thus there is the real possibility that Collembola could be added deliberately to the roots of glasshouse crops as a biological control agent for a variety of fungal diseases (Curl 1988; Curl and Snell 1981; Curl *et al.* 1985, 1988; Lartey *et al.* 1986, 1988, 1989, 1991, 1994).

In the majority of cases, grazing of fungi stimulates hyphal growth and fungal respiration (Bengtsson and Rundgren 1983; Bengtsson *et al.* 1993; Hedlund *et al.* 1991; Leonard and Anderson 1991b; Lussenhop 1992; Seastedt and Crossley 1980; Fig. 7.3). If selective, grazing may alter the relative abundance of different fungal species (Visser 1985). However, there is a tendency for the response to be 'bell-shaped' with intermediate densities of Collembola providing the greatest stimulation, although this is also affected by the condition of the fungus (Hanlon

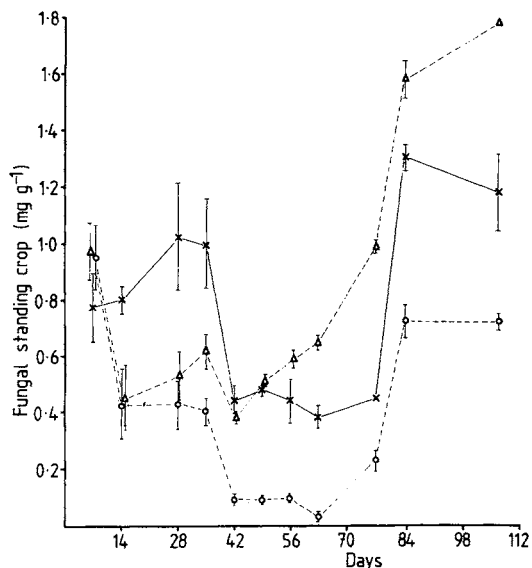


Fig. 7.3. Total fungal standing crop (mg g⁻¹) colonising leaf litter from *Folsomia candida* (Isotomidae) grazed (circles) and ungrazed (crosses) laboratory microcosms and the grazed fungal standing crop plus that consumed (triangles). The grazing activity of *Folsomia candida* generally stimulates fungal production. Reproduced from Leonard and Anderson (1991b) by kind permission of the authors and Gustav Fischer.

1981; Leonard 1984; Walsh and Bolger 1990; Fig. 7.4). In the field, the extent of stimulation or inhibition of fungal growth depends on the quality of the decomposing material, degree of processing by other organisms and length of time that the fungal matrix is maintained (Leonard and Anderson 1991a).

Fungi are extremely effective at concentrating ammonium, calcium, copper, phosphate and sodium ions from the substrate (Bååth 1991; Cromack *et al.* 1977; Visser *et al.* 1981). However, in metal-contaminated environments, the hyphae may contain concentrations of metals which are at least an order of magnitude higher than in the soil. Thus fungi are an important route for food chain transfer of metals and radioisotopes (Bengtsson *et al.* 1983; Borio *et al.* 1991; Hopkin 1994; Hove *et al.* 1990). To a certain extent, some species of Collembola can 'taste' very high concentrations of pollutants in contaminated hyphae and avoid them (Bengtsson *et al.* 1985b) but they will of course be wiped out through starvation if all fungi are rejected for this reason.

Why do some springtails show preferences for different species of fungi? There are two main reasons. First, they may 'choose' to eat one type because it is more nutritious, perhaps because the hyphae contain more protein (Usher *et al.* 1982). Indeed, *Folsomia candida* has a higher fecundity and rate of development if fed on some species of fungi than on others (Booth and Anderson 1979; Table 7.1). Second, they may avoid certain species because they contain poisons (Visser and

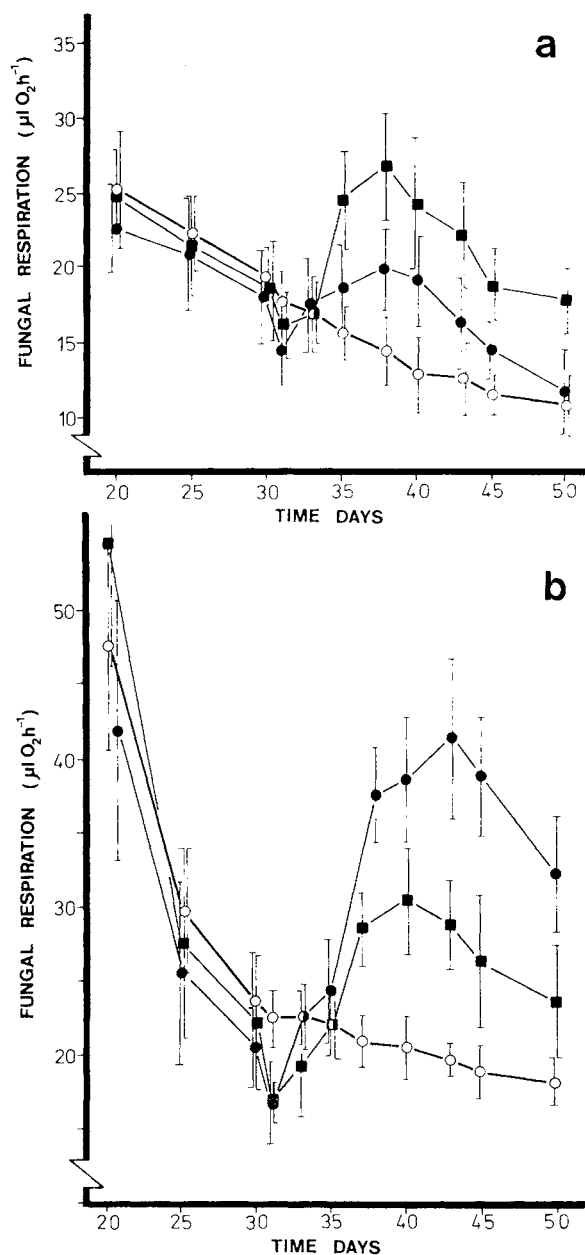


Fig. 7.4. Effects of grazing by *Folsomia candida* (Isotomidae) on respiration of senescent colonies of *Botrytis cinerea* grown on vermiculite granules containing (a) 33.36 g l⁻¹, and (b) 133.36 g l⁻¹ Czapek Dox. Collembola were added on day 30 of the experiments and respiratory rates for the animals were determined independently and subtracted from total respiration. Mean fungal respiration (\pm 95% confidence limits, $n = 5$) is shown for cultures containing 0 (open circles), 20 (squares) and 40 (filled circles) Collembola. Reproduced from Hanlon (1981) by kind permission of the author and *Oikos* Editorial Board, Lund, Sweden.

Table 7.1. Moulting rate and fecundity (mean \pm standard error) of *Folsomia candida* (Isotomidae) under different feeding regimes involving two species of fungi each grown under four concentrations of nitrogen. Reproduced from Booth and Anderson (1979) by kind permission of the authors and Springer-Verlag.

Feeding regime	Animal response	
	Moulting rate (exuviae wk ⁻¹)	Egg laying rate (eggs wk ⁻¹)
Starved	0.387 \pm 0.044	0.21 \pm 0.11
<i>Coriolus versicolor</i>		
2 ppm nitrogen	0.663 \pm 0.052	6.22 \pm 0.84
20 ppm nitrogen	0.752 \pm 0.061	10.84 \pm 1.18
200 ppm nitrogen	0.923 \pm 0.052	20.48 \pm 1.82
2000 ppm nitrogen	0.832 \pm 0.044	3.63 \pm 1.07
<i>Hypholoma fasciculare</i>		
2 ppm nitrogen	0.790 \pm 0.039	20.74 \pm 1.52
20 ppm nitrogen	0.929 \pm 0.044	28.31 \pm 2.36
200 ppm nitrogen	0.960 \pm 0.031	31.16 \pm 2.27
2000 ppm nitrogen	0.898 \pm 0.040	18.16 \pm 1.59

Whittaker 1977). *Protaphorura armata* prefers to eat hyphae containing the lowest concentrations of toxins (Shaw 1985). Indeed the extreme toxicity of the sporophores of fungi such as the Death Cap toadstool may have evolved to deter fungivory by euedaphic grazing animals (Usher *et al.* 1982).

The selectivity shown by some Collembola when grazing fungi has wide-ranging implications for soil ecology and agriculture (Moore 1988; Moore *et al.* 1988; McMillan 1976; Parkinson *et al.* 1979; Whittaker 1981; Wiggins and Curl 1979; Wiggins *et al.* 1979). An important study was conducted by Newell (1984a) in Grizedale Forest in the English Lake District. The fungi *Mycena galopus* and *Marasmius androsaceus* produced more than 99% of the fruiting bodies under the trees (*Picea sitchensis*). In the laboratory, *M. androsaceus* colonised litter from both the L and F1 horizons more than twice as fast as *M. galopus*, but in the field, the former species was restricted to the L horizon and the latter to the F1 horizon. '*Onychiurus latus*' (probably referable to *Protaphorura aurantiaca* (Ridley 1880) *sensu* Pitkin 1980) was the most abundant mycophagous arthropod at the field site and consistently had basidiomycete hyphae in its gut. In laboratory and field tests, '*O. latus*' showed a marked preference for the mycelium of *M. androsaceus* over *M. galopus* (also confirmed by Shaw 1988; Table 7.2). Thus the results strongly suggest that selective grazing by '*O. latus*' may be the main reason for the differing vertical distribution of the two fungal species in Grizedale Forest.

Furthermore, Newell (1984b) showed that *M. androsaceus* is a superior decomposer of spruce litter (17% weight loss over 6 months at 11°C) than *M. galopus* (11.5% under the same conditions). Thus not only is '*O. latus*' altering the distribution of fungi in the field, its selective grazing activity may be indirectly reducing the decomposition rate of the leaf litter. Fungal successions from primary sapro-

Table 7.2. Feeding preferences of *Protaphorura armata* (Onychiuridae) on agar discs incorporating different species of fungi in the laboratory (20 individuals in each treatment exposed for 5 days). Reproduced from Shaw (1988) by kind permission of the author and Gustav Fischer. Values indicated by the same letter are not significantly different (Walter–Duncan *t*-test).

Fungus	Mean fecal pellet count	Mean % area eaten
<i>Marasmius androsaceus</i>	74.8 ^a	72.2 ^a
<i>Laccaria proxima</i>	70.8 ^a	41.4 ^{b,c}
<i>Lactarius rufus</i>	64.5 ^a	55.7 ^b
<i>Suillus luteus</i>	48.9 ^a	50.7 ^b
<i>Mycena galopus</i>	19.2 ^b	68.2 ^{c,d}
<i>Suillus bovinus</i>	16.6 ^{b,c}	18.2 ^d
<i>Rhizopogon roseolus</i>	13.8 ^{b,c}	20.7 ^d
<i>Paxillus involutus</i>	13.1 ^{b,c}	21.3 ^d
<i>Mycena epipterygia</i>	10.6 ^c	24.2 ^d
<i>Pisolithus tinctorius</i>	2.1 ^d	0.2 ^e
<i>Clitocybe</i> sp.	1.1 ^d	1.2 ^e
<i>Hebeloma crustuliniforme</i>	1.0 ^d	1.7 ^e

phytes to secondary saprophytes of leaf litter may also be slowed down by preferential feeding of Collembola on primary saprophytes (Klironomos *et al.* 1992).

Seastedt (1984) predicted that selective fungal feeding by springtails would be shown to be extremely important in affecting populations of fungi associated with plant roots and indeed, this has proved to be the case (Thimm and Larink 1995). Recent laboratory experiments have demonstrated that the selective feeding activities of springtails on mycorrhizal symbionts and pest fungi can significantly affect the performance of the host plant.

Springtails have been shown to graze on essential vesicular arbuscular mycorrhizae (VAM) (Moore *et al.* 1985). For example, the presence of *Folsomia candida* in the soil of pot cultures of soybeans (*Glycine max*), in which VAM are essential for normal growth, resulted in 34% less mycorrhizal root length and 38% fewer infection sites than in controls without springtails (Kaiser and Lussenhop 1991). In leeks (*Allium porrum*), the grazing activity of *F. candida* on the essential VAM was sufficient to reduce the growth of the vegetable to little better than uninfected plants (Warnock *et al.* 1982). In experiments on the perennial mycorrhizal grass *Panicum virgatum*, Boerner and Harris (1991) showed that grazing of VAM by *F. candida* significantly decreased the root:shoot ratio and nitrogen concentration of the plants (Table 7.3). Other experiments have shown the effects to be density-dependent (Harris and Boerner 1990; Fig. 7.5). Thus the effects of mycorrhizal grazing may be detrimental, beneficial, or have no affect, depending on the species involved, their population densities and the experimental conditions (Finlay 1985; Klironomos and Kendrick 1995b; Setälä 1995).

The main conclusion of this Section is that Collembola are important in controlling fungal pests of agricultural crops, and influencing the levels of essential mycorrhizal infections. The widespread use of insecticides which kill springtails

Table 7.3. Growth and nutrient uptake of vesicular arbuscular mycorrhizae (VAM) inoculated and control (without competition) grass *Panicum virgatum* grown with or without *Folsomia candida* (Isotomidae). Means are given with standard errors in parentheses. *p*, level of significance of difference between means; ns, difference not significant at $p < 0.05$. Reproduced from Boerner and Harris (1991) by kind permission of the authors and Kluwer Academic.

Parameter	With Collembola		Without Collembola		<i>p</i>
Total mass (mg)	835	(80)	764	(112)	ns
Shoot mass (mg)	670	(66)	576	(93)	ns
Root mass (mg)	165	(16)	168	(32)	ns
Root: shoot ratio	0.25	(0.02)	0.36	(0.05)	0.05
N concentration (mg g ⁻¹)	18.22	(1.19)	28.57	(3.13)	0.01
P concentration (mg g ⁻¹)	3.20	(1.11)	2.85	(0.20)	ns
N : P ratio	8.11	(2.50)	10.22	(1.47)	ns
Total N mass (mg)	16.52	(2.67)	20.60	(6.46)	ns
Total P mass (mg)	2.73	(0.73)	1.89	(0.30)	ns

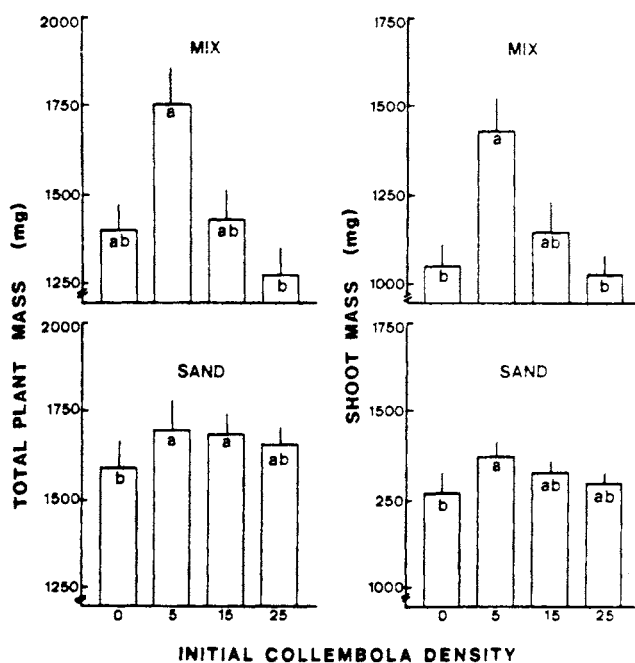


Fig. 7.5. Total plant mass and shoot mass (mg) of *Geranium robertianum* in relation to initial density of *Folsomia candida* (Isotomidae) in sand and high organic greenhouse mix. Each histogram bar represents the mean of 12 replicates (vertical bars = one standard error of the mean). Bars labelled with the same letters were not significantly different at $p \leq 0.05$. Reproduced from Harris and Boerner (1990) by kind permission of the authors and Kluwer Academic.

may be having indirect detrimental effects on the growth of crops which are of considerable economic importance.

7.3 Interactions between Collembola and other animals

7.3.1 Predators of Collembola

Each summer there is a mass migration of hundreds of juvenile toads from my pond in Reading to all parts of the garden. For several weeks, the toads can be observed hopping about in search of prey among dead leaves which collect in the corners of the garden. If one watches closely, the young toads can occasionally be seen catching specimens of *Orchesella villosa* which crawl over the surface of the leaf litter. I have also seen blackbirds and robins eating *O. villosa*, and the equally common *Pogonognathellus longicornis*. The birds are quite tame. If I lie quite still, they will approach to within 1 m of me as they work their way through the borders, catching springtails disturbed by their feeding activity among the leaf litter.

There is quantitative information to support the importance of vertebrates as predators of Collembola. Betts (1955) examined the stomach contents of birds in English woodland. He found a Marsh tit with 211 unidentified springtails in its gut and a Blue tit with 41 specimens of *Entomobrya nivalis* in its stomach. Gasc *et al.* (1983) found that 30–48% of the prey items of small lizards in parts of French Guyana were Collembola on which the reptiles appeared to prey selectively.

Nevertheless, the majority of springtails fall victim to other arthropods (Christiansen 1971a; Ernsting and Joosse 1975; Van Straalen 1985c). Many of these predators such as harvestmen (Opiliones), hunting spiders, pseudoscorpions and ants are generalists that will eat springtails if they happen to come across them (Dejean 1985; Foster 1970; Hölldobler and Wilson 1990; Johnson and Wellington 1980b,c; Schlegel and Bauer 1994). *Janetschekbrya matthewsi* (Entomobryinae) was described as a new species by Snider (1981c) and was found in the 'larder' of a sphecoid wasp where it had been stored by the adult for its larvae.

Euedaphic Collembola in which the furca is reduced or absent, and eggs and juveniles of hemiedaphic and epedaphic species in the soil, are particularly vulnerable to predation by mites (Knight and Read 1969; Krogh 1995b). Onychiurinae, which have no furca, have evolved defensive glands in response to predation pressure (Section 4.2.4). In Antarctica, carnivorous mites have been shown to predate almost exclusively on Collembola (Block 1985a; Lister *et al.* 1987, 1988; Usher and Bowring 1984; Usher *et al.* 1989).

Many beetles are specialised to prey specifically on Collembola and have evolved very efficient trap mechanisms to catch them before they jump, or to prevent their escape (Fig. 7.6). These mechanisms include the sticky labium of the staphylinid *Stenus comma*, which is specialised for the capture of small springtails (Bauer and Pfeiffer 1991), and the setal and antennal traps of carabids (Bauer 1982a, 1985; Hintzpeter and Bauer 1986). Nevertheless, not all species are caught with the same degree of success. The beetle *Loricera pilicornis* is able to retain

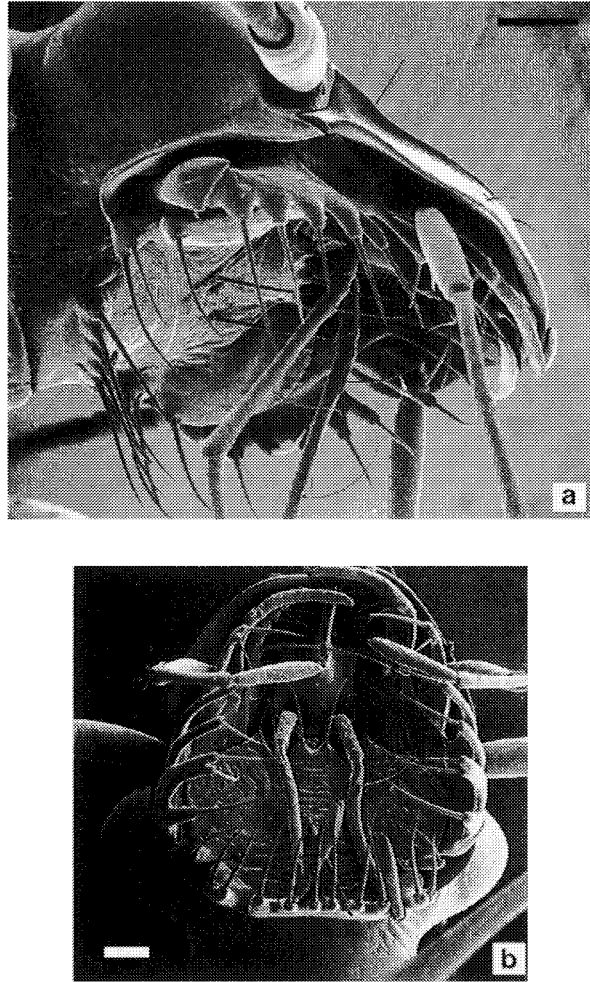


Fig. 7.6. Scanning electron micrographs of the setal trap of the mouthparts of the carabid beetle *Leistus sardous* viewed from the side (a) and below (b). This structure has evolved to catch mainly Collembola. Scale bars = 200 μm . Reproduced from Bauer (1985) by kind permission of the author and Gustav Fischer.

Heteromurus nitidus in its antennal trap but when *Sminthurus viridis* attempts to escape, this springtail develops enough kinetic energy during a jump to bend the setae and win its freedom (Hintzpeter and Bauer 1986).

One of the most common springtail-specific predators is the carabid beetle *Notiophilus biguttatus* (Davies 1967; Ernsting and Jansen 1978; Evans and Forsythe 1985; Higgins 1982). Indeed, Ernsting and Joosse (1975) detected the highest radioactivity in this species of all predatory arthropods 18 days after releasing specimens of *Orchesella cincta* and *Tomocerus minor* labelled with ^{32}P into woodland soil. Larvae and adults of *N. biguttatus* search out aggregations of

springtails using chemical cues (Bauer 1982*b*). When a springtail is detected with its large compound eyes, the beetle moves forward until the forward-projecting trichobothria touch the prey. It then lunges forward snapping the mandibles shut. In experiments with *O. cincta*, the beetle was successful about 50% of the time (Ernsting and Fokkema 1983). Many of the springtails which escaped had damaged antennae. Such damage is frequently observed in specimens of *O. cincta* collected from the field (Lubbock 1873).

Thus there have been strong selective pressures for epedaphic and hemiedaphic springtails to minimise the time between detecting danger and leaping to safety. The evolutionary race between the speed of prey capture mechanisms in beetles and the jumping response time of springtails has been won to a large extent by the beetles. However, sufficient springtails escape for large populations of Collembola to persist in most terrestrial ecosystems.

7.3.2 Parasites of Collembola

Few workers have set out deliberately to document the parasites of springtails. Most observations have been incidental to taxonomic descriptions or ecological surveys. External parasitism is apparently very rare. Miles (1976) found two Protura with their mouthparts embedded in the tissues of two specimens of *Isotoma viridis* (out of 2719 individuals examined), and also observed nematodes attached to the external surface of *Orchesella villosa* Miles (1971). Ectoparasitic fungi are also present in some cave Collembola (Christian 1990). I have occasionally found mites attached to the legs and body of *Orchesella villosa* but these were probably phoretic ('hitching a ride') rather than strictly parasitic.

Internal parasites are more common. Microsporidia and other Protozoa have been found in a wide range of species (Maddox *et al.* 1982; Manier and Bouix 1981; Purrini 1982, 1984*b*). Interestingly, the rates of infection are much higher in springtails from forests subject to high levels of sulphur dioxide deposition suggesting that their resistance is weakened by the pollution (Purrini 1983, 1984*a*). Gregarines were found in the midgut epithelium of a species of *Isotoma* by Eisenbeis and Meyer (1986) but were apparently doing little harm. In contrast, Miles (1974) observed large nematodes in *Protaphorura armata* and included a photograph in which the whole body cavity of the springtail is filled with four of the parasites. This would definitely be fatal. Nematodes have also been found in *Neanura grassei* (Phillips 1946).

Collembola harbour pathological fungi (Leatherdale 1958), but many of the hyphae which are often seen protruding from dead springtails in the field probably belong to saprophytic rather than parasitic species.

The inescapable conclusion is that parasitism is not a significant cause of mortality in Collembola in comparison to predation. In light of the heavy predation pressure on springtails described above, one would expect *a priori* for Collembola to be intermediate hosts for a wide range of internal parasites. However, there is only one tentative record of springtails acting as intermediate hosts, and that is for a tapeworm (Kozlov 1986). The role of Collembola as intermediate hosts for parasites would clearly make an excellent topic for further research.

7.3.3 *Non-parasitic interactions between Collembola and other animals*

There is no convincing evidence that any springtail is an obligate parasite. Nevertheless, Collembola do interact with many other terrestrial invertebrates. For example, the nymphs of some oribatid mites carry the discarded exoskeletons of Collembola on their backs, presumably as camouflage (Norton and Ryabinin 1994). Springtails are often found in the nests of small mammals (Davis 1934; Hrivnak 1983), bumblebees (Snider and Husband 1966) and birds where they can be quite numerous.

Many species of Collembola occur in the nests of eusocial insects where they are tolerated by their hosts and sheltered from climatic extremes and predators (Stebaeva 1989*b*). The springtails apparently do no harm and appear to feed on detritus within the nests which would probably be thrown out anyway (Hölldobler and Wilson 1990). Some species are facultative guests and can be found away from their hosts (Ellis 1967; Rusek 1971). However, members of the Cyphoderidae are specialised for this lifestyle and are found only in the nests of termites (Ashraf 1969; Handschin 1924; Paclt 1965) and ants (Hölldobler and Wilson 1990; Stebaeva and Grishina 1983).

If the host insect becomes extinct, then so may the Collembola that live in the nest. Yoshii (1989*a*) described how he went in search of *Lepidosinella armata* (Entomobryinae) which Handschin had described from termite mounds in East Java. Unfortunately the site had been converted to an apple plantation. The termites had vanished and so had *L. armata*.

7.3.4 *Interactions between Collembola*

There is very convincing evidence for the release and detection of pheromones by Collembola. Aggregation pheromones are produced by several species including *Sinella coeca* (Tosi *et al.* 1977), *Orchesella cincta* (Mertens *et al.* 1979), *Heteromurus nitidus* (Krool and Bauer 1987) and *Hypogastrura viatica* (Mertens and Bourgoigne 1977). The main function of aggregation pheromones is to attract the opposite sex (Joosse and Koelman 1979; see also Section 8.3). However, non-sexual attraction may be selectively advantageous in promoting aggregation at rich sources of food. Closely aggregated Collembola may also create their own microclimate and be less prone to desiccation.

Perception of an aggregation pheromone is not strictly species-specific, although all species that have been tested are more responsive to their own pheromones than those produced by others (Verhoef *et al.* 1977*a,b*). Some species synchronise their behaviour by moulting simultaneously in response to a pheromone (Leinaas 1983*b*). Others may release an alarm pheromone in response to danger which induces increased activity, and presumably increases the chances of escape (Purrington *et al.* 1991). Pheromones are present in the faecal pellets and the digestive tract may be the main site of secretion (Verhoef 1984). Other possible sources include the anal sacs (Leinaas 1988). However, as far as I am aware, no one has studied the chemical nature of collembolan pheromones.

Laboratory studies on interactions between different species of Collembola (and with other soil arthropods) invariably come under the heading of 'competition' (Van de Bund 1972). These experiments are interesting in themselves and can contribute theory to population biology. However, the results are difficult to extrapolate to the field for many reasons (Christiansen *et al.* 1992). Species may be placed together that are unlikely to come across each other in the wild (Walsh and Bolger 1993). Predators are absent and climatic variations are minimised (constant or regularly fluctuating temperature and light regimes are usually employed; Longstaff 1976). Diets are very simple and if the springtails dislike the conditions, they are unable to migrate to a more favourable environment. Experiments have definitely demonstrated that competition occurs under strictly defined conditions in the laboratory but, in my view, it is not legitimate to extrapolate these results to complex natural environments.

In temperate climates, the soil, leaf litter and vegetation of a mature deciduous woodland typically supports about 30–40 species of Collembola. In warmer climates there may be 100 species or more. However, it is not difficult to envisage at least this number of niches when all possible combinations of discriminating factors are considered. These include preference for a euedaphic, hemiedaphic or epedaphic lifestyle, diet (Vannier 1979*b*, 1985), activity period, oviposition site and many more. I may be wrong, but it seems unlikely to me that competition between springtails is of major ecological importance in controlling the distribution of different species of Collembola.

In contrast to competition, a beneficial situation may arise when the presence of one species improves the performance of another compared to the species on its own (Christiansen 1967). For example, when I have tried to keep *Isotoma viridis* in standard laboratory conditions (moist plaster of Paris, brewer's yeast as a food source), the population dies out within a few weeks. However, if a few adults of *Folsomia candida* are added, *I. viridis* thrives and both species reproduce and maintain viable populations for several months. The explanation for this result is not known. Perhaps *F. candida* conditions the yeast in such a way that their faeces provide a more favourable diet for *I. viridis*? Maybe *F. candida* grazes a fungus that grows on the eggs of *I. viridis*? There are clearly many relationships between Collembola remaining to be discovered.

7.4 The roles of Collembola in decomposition processes

As plant and animal remains decay, most of the nutrients released are eventually assimilated by the roots of living vegetation. Decomposition processes are strongly influenced by the microbes, fungi, Protozoa, and animals which live in soil and leaf litter habitats (Anderson and Ineson 1984; Aranda *et al.* 1990; Petersen *et al.* 1985). Collembola are numerous in terrestrial ecosystems and play several important roles in decomposition processes. Consumption of dead vegetation, and its subsequent excretion as partially-decomposed faecal pellets, increases the surface area and suitability of the material for microbial and fungal attack (Hasegawa and Takeda 1995; Koledin *et al.* 1981; Takeda 1988; Van Amelsvoort

et al. 1988; Zinkler 1983). Direct grazing of hyphae may inhibit or stimulate fungal growth and may influence the distribution of particular species (Anderson and Ineson 1983; Bakonyi 1989; Hanlon and Anderson 1979; Visser 1985; Section 7.2.4). Springtails are also responsible for redistributing plant material, and viable fungal spores and bacteria, when they feed in one litter or soil horizon and defaecate in another (Anderson 1988; Hassall *et al.* 1986b; Rusek 1975a; Santos and Whitford 1981).

The fundamental question to ask is 'what would be the effect on decomposition in a particular habitat if Collembola were to be totally removed?' One experimental approach which has been employed to answer this question is to compare the decomposition rate of leaf litter held in microcosms in the laboratory, with and without Collembola (Hågvar 1988; Teuben 1991; Teuben and Roelofsma 1990; Teuben and Verhoef 1992a). Most of these experiments have shown that enzyme activity, respiration (measured by oxygen consumption or carbon dioxide production) and rates of nutrient release from leaf litter are stimulated in the presence of low to moderate (natural field) densities of Collembola (Dorel and Verhoef 1987; Faber *et al.* 1992; Ineson *et al.* 1982).

The answer to the question posed above is that in the absence of Collembola, the rates of some decomposition processes slow down. Whether or not this makes a significant difference to rates of decomposition in the field depends on the proportion of the total fauna that is Collembola. Thus in temperate grasslands and deciduous woodlands where earthworms are abundant, the total contribution of Collembola to decomposition is probably small (Petersen and Luxton 1982). Springtails are relatively more important in acidic or polluted environments from which earthworms are absent (Stebaeva 1989a).

It is very difficult to give an overall figure as to the proportion of total litter fall that springtails are directly responsible for decomposing. Petersen (1994) concluded that in most ecosystems, Collembola metabolise 0.1–1% of above-ground plant litter production, although the figure was 2.7% in two forest sites. However, Van Straalen (1989) estimated that the Collembola in a pine forest in The Netherlands were responsible for consuming 6% of the annual litter fall. The disparity in these figures reflects the different assumptions of assimilation efficiency, feeding rates and other parameters and the figure could in fact be greater than this, possibly as high as 20% (Petersen 1994). More research is needed on this topic. In Antarctic tundra where the diversity of the soil fauna is restricted to a few species of springtails and mites, the role of Collembola in decomposition is very important; their absence would have significant consequences for the long-term productivity and integrity of this polar ecosystem.

Measuring overall decomposition rates of leaf litter masks the more subtle effects of Collembola grazing (Andrén and Schnürer 1985). Springtails may be of greater relative importance in early stages of decomposition when there is fairly rapid succession of different species of fungi, each adapted to exploit a specific substrate (Ponge 1991b). These fungi are rich sources of nutrients for springtails and they will graze the hyphae in preference to ingesting leaf material (Hågvar and Kjølndal 1981a).

Teuben and Verhoef (1992*b*) calculated that faeces production by Collembola resulted in a 2.4-fold increase in the availability of nitrates in pine forest soils. Nutrients released from decomposing litter, which percolate down through the soil, are assimilated with high efficiency by the fine roots of plants, especially their mycorrhizal fungi (Faber 1991*b*). Thus, selective grazing on mycorrhizae by Collembola may affect nutrient fluxes by suppressing or promoting the growth of these root symbionts (Seastedt 1984). Faber and Verhoef (1991) demonstrated these effects in a pine plantation (*Pinis nigra*) in The Netherlands using field enclosures from which all other soil fauna had been excluded. In the presence of *Orchesella cincta*, a net loss of 310 mmol m⁻² of total nitrogen from the plots was observed in comparison to the control which gained 76 mmol m⁻² of nitrogen. However, it was shown that at least half of the leachable nitrogen was intercepted and assimilated by tree roots as it passed down the soil profile.

In the most recent review of the topic, Petersen (1994) concluded that the main effects of Collembola on decomposition are the stimulation and inhibition of the activities of microorganisms. However, at present, there is too little information available to quantify these effects under all field conditions. A general conclusion would be that the selective feeding activities of springtails increase the rates at which nutrients are released from decomposing vegetation, and stimulate microorganisms and fungi and hence the nutrient retention capacity of the litter layer (Seastedt and Crossley 1980; Verhoef and De Goede 1985; Verhoef *et al.* 1989). However, the work on which these conclusions are based has been conducted in temperate ecosystems; a different situation may exist in tropical regions which have hardly been studied (Lavelle *et al.* 1993).

7.5 Collembola as pests

Given their ubiquitous distribution and abundance, it is perhaps surprising that Collembola do not impinge more on human activity than they do. Apart from a few minor cases involving individual people (Greenberg 1985; Scott *et al.* 1962; Section 1.2), the main impact of springtails on the human population is when they feed on our crops.

A pest is a species of animal or plant which exists where humans do not want it to (but see thought-provoking paper by Kellert 1993). The first mention of springtails as pests is in the book *Farm Insects* by John Curtis (1860) in which the deleterious effects of direct feeding on seedlings by the 'potato ground flea' were described. Curtis called this '*Smynturus solani*' but he was probably referring to *Bourletiella hortensis*, or a closely-related species in the same genus.

Theobald (1910) listed 23 species of Collembola as being 'distinctly injurious' and provided numerous examples of springtails feeding on crops in several countries. However, many of these early records simply record associations of springtails with damage. Most species are falsely accused of being pests because they are attracted to wounds created by slugs or other primary herbivores. Indeed there was a tendency at the beginning of the century to assume that whenever insects were discovered in large numbers on crops, they were the cause of the damage and

should be exterminated. It is a wonder that anything (including gardeners!) survived the onslaught of pesticides containing arsenic, lead, copper and other toxic metals dispensed from a variety of ingenious spraying devices like those illustrated in advertisements in Theobald (1909).

However, there are a few species of Collembola which definitely eat agricultural crops. Onychiurids may nibble the roots of plants (Getzin 1985). *Bourletiella hortensis* damages seedlings by nibbling at the bases of the stems just above soil level (Davies 1926; Stenton 1922). This 'disease', known as 'black leg' or 'strangle', occurs in mangolds (Davies 1925), conifers (Marshall 1978; Marshall and Ilnytsky 1976; Marshall *et al.* 1990) and sugar beet (Honma 1988). Before the advent of modern insecticides, *B. hortensis* was controlled by dragging a tar-covered blanket through the crops on to which the springtails became stuck in their millions (there is a photograph of this apparatus in Davies 1926).

Sminthurus viridis (see Fig. 2.6) is probably the most economically important pest collembolan (Davies 1928a; Greenslade and Ireson 1986). It feeds on low growing plants, especially clover and lucerne, the source of its more common name, the 'Lucerne flea'. Where it has been introduced in the Southern Hemisphere, *S. viridis* can decimate fields of crops if not controlled (Davidson 1934; Walters 1968). About 10% of spring-sown oil poppies (*Papaver somniferum*) in the north of Tasmania are sprayed to control *S. viridis* (Ireson 1993). Densities in excess of 50 000 m⁻² have been recorded in Tasmanian pastures (Ireson and Paterson 1991). Holdaway (1927) quoted this species as being 'the most important insect pest of field crops in South Australia'.

Formerly a Northern Hemisphere species, *S. viridis* is now distributed in two parallel bands, one north and the other south of the Equator where climatic conditions are suitable (Maclagen 1932). Its northern limits in Norway and Finland are defined by a line corresponding to localities experiencing 100 consecutive days during the year on which the temperature exceeds 10°C. Its southern limits in Spain and Morocco are defined by a winter (November to April inclusive) isohyet of 250 mm, the same line which defines the limit of its distribution in Australia (Wallace 1973).

In Australia, the distribution of *S. viridis* is limited by temperature, mean monthly rainfall (R) and evaporation (E). The ratio R/E = 1 is the critical value below which dryness may prevent the occurrence of the active stage. When the ratio greatly exceeds 1, excessive wetness, particularly when accompanied by mean monthly temperatures of less than 10°C, severely restricts population growth owing to retarded development and high death rate (Davidson 1933b). Ideal conditions for most rapid population growth are a temperature of 25°C, and 60–80% saturation of the soil. Below 50% or above 80% soil moisture very few eggs hatch because they dry out or become waterlogged (Davidson 1933a).

The main method of control of *S. viridis* is to spray with insecticides. Nevertheless, alternative methods not involving pesticides have been attempted. One approach is to attack the egg stage and to create conditions which are unsuitable for the adults. The eggs of *S. viridis* are laid in the soil surrounded by a faecal

coat and are quite intolerant of alkaline environments. Thus Holdaway (1927) recommended the following farming practices to reduce their incidence:

- Bare fallowing in the rotation so the adults have nothing on which to feed.
- Liming of the soil, which kills the eggs.
- Keeping headlands free of vegetation to prevent *S. viridis* from using these sites as a refuge.

Another method of biological control is to promote native natural enemies or to introduce species which prey on *S. viridis* in their European homeland (Ireson and Paterson 1991). Most attempts have focused on the use of predatory mites (Ireson 1982, 1984; Wallace 1974; Wallace and Mahon 1971). Although they do not wipe out *S. viridis* completely, the predation pressure reduce the populations to much lower levels of abundance (Womersley 1933).

It should be pointed out that the '*S. viridis* problem' was created in the first place by the (admittedly accidental) human introduction of the species to areas where there were few natural enemies. Indeed, of the 59 species of Collembola listed by Greenslade and Ireson (1986) from the 'culture steppe' of Australia (areas modified by human activity from their original vegetated condition), only eight were considered to feed directly on live plant material of relevance to agriculture, and were candidates for control measures. All of these species were almost certainly introduced to Australia from other countries. Greenslade and Ireson (1986) concluded that *S. viridis* is the only significant collembolan plant pest in Australia.

Euedaphic species such as *Protaphorura armata* may become pests if there is no decaying vegetation on which they can feed. In such a situation, it is not surprising that they nibble the roots of plants such as tomatoes (Brown 1954), carrots (Murray 1877), and sugar beet (Joosse and Koelman 1979; Hurej and Pomorski 1989; Sievers and Ulber 1990). Nevertheless, the extent of their attack is often too low to cause noticeable economic damage (Hurej *et al.* 1992). Mushroom beds often become infested with large populations of Collembola. In sewage beds, population explosions of hypogastrurids are beneficial as the springtails help to degrade the organic matter through their feeding activity (Lawrence 1970a).

Whether an animal is considered to be benign, beneficial, or a pest depends on its density. Thus grazing by small numbers of *Folsomia candida* on mycorrhizal fungi of the roots of the forest herb *Geranium robertianum*, stimulates fungal growth and improves the performance of the plants in comparison to ungrazed controls (Harris and Boerner 1990). However, at high densities of *Folsomia candida*, plant growth is suppressed.

Many fungal spores remain viable after passage through the guts of Collembola (Poole 1959). Thus, springtails may be responsible for transmitting pathogenic fungi if they feed on a diseased plant then move to another healthy one on which they deposit faeces (Whipps 1993; Whipps and Budge 1993). However, in some situations, Collembola graze plant pathogenic fungi and reduce the severity of disease in cotton (Lartey *et al.* 1994) and cucumbers (Nakamura *et al.* 1992).

The vast majority of Collembola do little harm to crops. Their role in promoting decomposition processes and mycorrhizal development of plants, and in suppressing fungal diseases suggests that in most situations Collembola are beneficial. However, there is no doubt that a few species, such as *S. viridis* in Australia are economic pests (Greenslade and Ireson 1986; Ireson 1993). But this is no reason to tar them all with the same brush (or blanket!). The widespread use of broad spectrum insecticides should be discouraged.

Reproduction, development and life histories

8.1 Introduction

Natural selection favours early breeding, high fecundity and low mortality rates, other things being equal. If other things are not equal, trade-offs exist between these life history variables. Collembola exhibit a wide range of development times, fecundities and life spans which do not appear to have a taxonomic basis. The life history characteristics of each species of springtail have evolved in response to selective pressures in the environment which have maximised their fitness for the particular ecological niche in which they reside.

Since the earliest detailed studies on life history characteristics of Collembola (e.g. Milne 1960), a huge number of papers has been published on fecundity, development times, moulting frequency and longevity in different species. There is tendency for euedaphic species which live in the more stable predictable soil environment to be parthenogenetic and to have relatively few large offspring which are produced over an extended reproductive period. In contrast, epedaphic species are invariably sexually reproducing with large numbers of small offspring produced during well-defined reproductive periods which are synchronised with the climate (Petersen 1980; Van Straalen and Van Diepen 1995).

Species with flexible life histories are able to thrive in a wide range of habitat types and may have large geographic ranges (Joosse 1969). For example, Ernsting *et al.* (1993) showed that within a population of the common and widespread epedaphic species *Orchesella cincta*, individuals exhibited great flexibility in certain aspects of their life histories depending on the quantity and quality of food available. There was a range from some which were fast growing, small and lived for only a short time, to others which were slow growing, large and long-living.

Other species are opportunists and are able to exploit temporary habitats in which they undergo massive population explosions. One cause of 'swarming' may be the sudden availability of an abundant and ideal food source. In an experiment conducted at Rothamsted, England in 1936, four soil plots, each approximately 8 m³ in area, were sterilised by heating to 100°C (Baweja 1939), sown with grass seed and left to be recolonised by animals from the surrounding unsterilised soil. The normal population density of *Ceratophysella armata* (Hypogastrurinae) in the plots before treatment was about 7500 m⁻². However, immediately after sterilisation, the density rose to 150 000 m⁻², before declining back to normal over the next 6 months. This population increase was presumably a 'knock-on' effect of the presence of large amounts of dead plant and animal remains (including saprophytic fungal hyphae) on which *C. armata* was able to feed *ad libitum*. The initial

absence of predators in the sterilised soil may also have contributed to the massive early population growth. This example, together with others such as the huge abundance of *Collembola* on dung (Thome and Desière 1975), serves to illustrate that some species of *Collembola* are opportunists which are able to exploit ideal conditions as and when they arise in the field.

One could write a whole book on the theoretical basis of the different life history strategies of springtails. However, in a general text such as this, I do not think it appropriate to present such a detailed discussion. Further information can be found in Stamou *et al.* (1993) and Witteveen and Joosse (1987). In this Chapter, the structure and function of the testes and ovaries and their respective gametes are reviewed (Section 8.2), mating, fertilisation and egg-laying behaviour are covered (Section 8.3) and the development of the embryo up to and including hatching is described (Section 8.4). Postembryonic development into the mature adult stage is examined in detail (Section 8.5) and the phenomena of ecomorphosis, epitoky and cyclomorphosis, when *Collembola* enter a 'dormant' stage, are outlined (Section 8.6). Finally, the ratios between sexes are discussed together with a consideration of parthenogenesis where some species of *Collembola* are able to reproduce in the absence of males (Section 8.7).

8.2 Reproductive organs, gametes and chromosomes

8.2.1 Male gametes and reproductive organs

Collembola have separate sexes and indirect sperm transfer. The sperm are produced from paired testes and ejaculated from a simple genital opening (see Fig. 4.1) in a spermatophore which is deposited on the substrate, or placed directly on the female genital opening. A variety of mechanisms have evolved to ensure successful 'capture' of this spermatophore by the female (Section 8.3).

The sperm of *Collembola* consist of four main parts (Fig. 8.1). The *peduncle* attaches the sperm to the wall of the testis but is otherwise of unknown function. The *acrosome* is distal to the peduncle and is followed by the elongate *nucleus*, and *axoneme* which has a 9+2 arrangement of microfibrils (Dallai 1974a, 1979a, 1994a; Jamieson 1987). In *Anurida maritima* the spermatozoan is 60 μm in length and is wound into a spiral with up to six turns, the whole complex being surrounded by granular material and a membrane (Fig. 8.1). This arrangement is substantially similar in other *Collembola* that have been examined (Dallai 1967b, 1970c; Krzysztofowicz 1967a; Krzysztofowicz and Byczkowska-Smyk 1966).

8.2.2 Female gametes and reproductive organs

The paired ovaries of *Collembola* are sac-shaped and are not composed of discrete ovarioles (Bilinski 1976; Krzysztofowicz 1971, 1977; Matsuzaki 1973; Paléovody 1976). However, in some springtails such as species of *Orchesella* they may be secondarily divided into two irregular lobes (Bilinski 1993). Each ovary is divided into two main regions, the *germanarium* which contains chain-like clusters of germ cells, and the *vitellarium* where the central cell of each chain differentiates

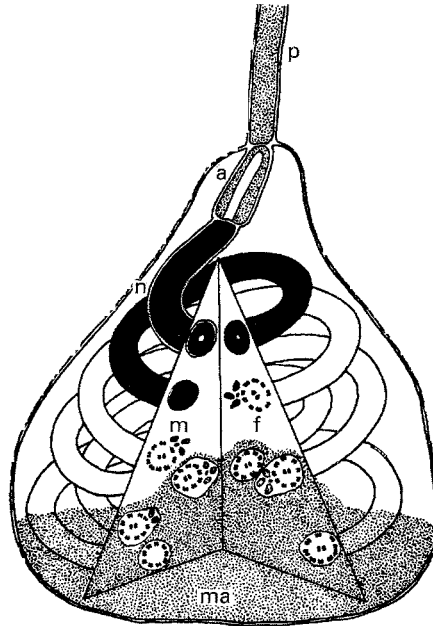


Fig. 8.1. Schematic diagram of a spermatozoon of *Anurida maritima* (Neanuridae). a, acrosome; f, flagellum (axoneme); m, mitochondria; ma, granular material; n, nucleus; p, peduncle. Reproduced from Dallai (1970c) by kind permission of the author and Professor B. Bacetti, University of Siena.

into an oocyte and is nourished by nurse cells on either side (Jablonska *et al.* 1993). Germ cells form early on in embryonic development (Jura 1967a; Krzysztofowicz 1980b; Szklarzewicz and Klag 1986; Tamarelle 1979) and are 'nurtured' by surrounding nurse cells which eventually degenerate (Adamiec 1975; Dallai 1967a). The nurse cells synthesize rRNA that is transferred to the developing oocytes. Lipid droplets, yolk spheres and other granular material is deposited in the oocytes which become surrounded by an egg envelope secreted by the follicular cells or the egg itself (Kisiel *et al.* 1994; Krzysztofowicz and Antoniklema 1981; Krzysztofowicz and Kisiel 1986, 1989; Larink and Bilinski 1989). A detailed review of this process has recently been published by Bilinski (1993). Development of the eggs may be affected by the presence of microorganisms (Palévody 1972, 1977).

8.2.3 Chromosomes

Collembola have small numbers of chromosomes. Apart from *Podura aquatica* in which $n = 11$ (haploid number), all other springtails have fewer than $n = 9$ (Brummer-Korvenkontio and Saure 1969; Hemmer 1990; Kiauta 1970; Saitoh and Chiba 1959). Species differ in the proportions of metacentric and acrocentric chromosomes and fusion or splitting has undoubtedly occurred throughout

collembolan evolution. Thus the use of the karyotype for phylogenetic reconstruction is questionable.

Intraspecific comparisons have been made in the banding patterns of polytene chromosomes in the salivary glands of neanurids (Dallai *et al.* 1983). Such information may be useful for separating geographic races of the same species which are otherwise morphologically identical (see Figs. 5.5, 5.6).

8.3 Mating behaviour and oviposition

8.3.1 Spermatophores

A spermatophore is a 'packet' of sperm produced by the male (Krzysztofowicz 1980a; Schliwa 1965). In *Dicyrtomina ornata*, the spermatophore is 45 μm in diameter and contains about 600 spermatozoa (Dallai 1975b). In some Collembola, the droplet of sperm is surrounded by a resistant coat which protects against desiccation (Klauer 1975). In other springtails, in which the spermatophore is produced shortly before acceptance by the female, the surrounding coat may be very thin or even non-existent (Blancquaert and Mertens 1977; Dallai 1975b). Several species fertilise the females by direct transfer of sperm to the genital aperture of the female and have no need for an elaborate spermatophore (Hale 1965a,b).

The spermatophore is often held above the substrate on a thin stalk which may extend into the sperm droplet or be expanded into a small ledge to provide support (Cassagnau 1971d; Fig. 8.2a). In some species, several spermatophores may be produced at once and are attached to the tips of a branching structure (Cassagnau 1971c). The sperm, and material for producing the stalk of the spermatophore, are both produced by the testes (Witalis 1993). In *Orchesella cincta*, the sperm and stalk secretion are separated in the ejaculatory duct which also produces the material for the outer coat (Doering 1986; Fig. 8.2b). Males of this species produce a mean of five spermatophores per day at 20°C but do this only for about half the intermoult period; spermatophores are deposited only in alternate instars (Joosse *et al.* 1973; Joosse and Veltkamp 1970). In *Sminthurus viridis*, the spermatophore is produced by pressing the genital plate against the substrate, secreting the mixture of sperm and supporting fluids, then raising the abdomen to form the stalk (Fig. 8.3).

Selective breeding experiments can be conducted by providing specific females with spermatophores derived from males with a known genetic history. This approach has been useful for examining genetic resistance to metal pollution in Collembola from contaminated environments (Posthuma *et al.* 1993a).

8.3.2 Sexual dimorphism

In most families of Collembola, conspicuous sexual dimorphism is rare. Females may be larger than males of the same age if they are full of eggs. However, it is difficult to sex most springtails without referring to the genital plate which can only be seen at high magnification (Betsch-Pinot 1974a,b; Betsch 1965b; Christiansen 1958a; Fig. 4.1).

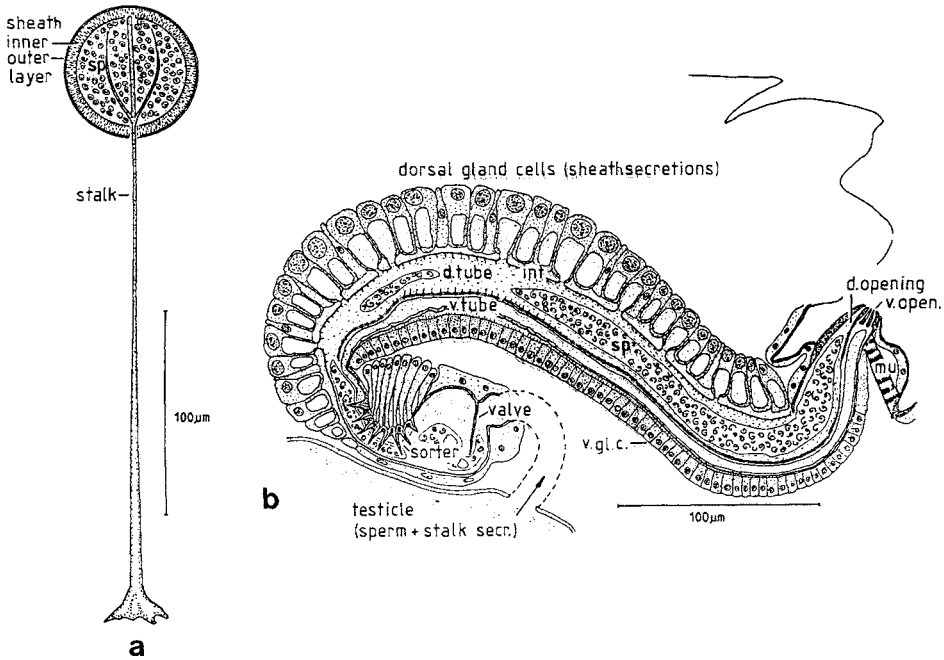


Fig. 8.2. Semi-schematic diagrams of (a) spermatophore and (b) ejaculatory duct of *Orchesella cincta* (Entomobryidae). Reproduced from Doering (1986) by kind permission of the author and the University of Siena.

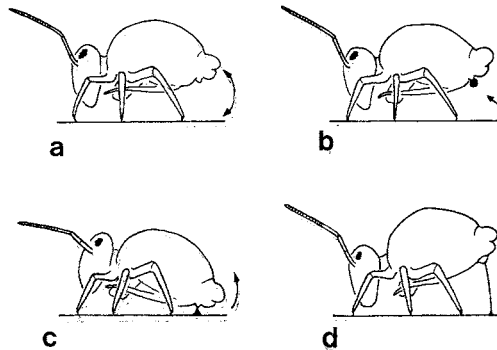


Fig. 8.3. Four stages of spermatophore production in *Sminthurus viridis* (Sminthuridae). (a) Exploration of the substrate; (b) extrusion of stalk material; (c) attachment of stalk material to substrate; (d) 'drawing out' of stalk material and extrusion of sperm droplet. Reproduced from Betsch-Pinot (1976) by kind permission of the author and Blackwell Wissenschafts-Verlag, Berlin.

In some species, the males exhibit relatively subtle secondary sexual characteristics such as longer or shorter setae on the body in comparison to the female and extra spines on the legs (Bellinger 1962; Betsch and Cassagnau 1966; Deharveng 1976a; Fjellberg 1973a,c; Gisin and Gama 1962; Mari Mutt 1981d; Massoud and

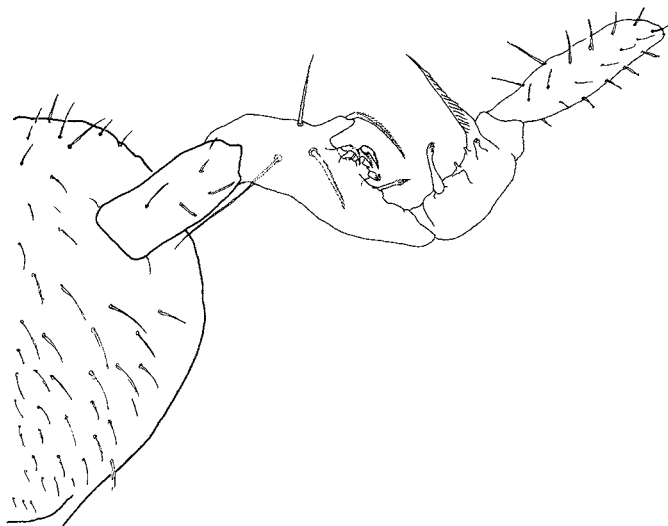


Fig. 8.4. Antenna (animal's left side) of male *Sminthurides aquaticus* (Sminthuridae) showing adaptation of the 2nd and 3rd sections to form a 'clasping organ' for holding the antennae of the female during mating. Redrawn after Massoud and Betsch (1972) by kind permission of the authors and Editions Gauthier-Villars.

Najt 1974, 1975). These features may only appear in the mating season and may be connected with mating behaviour or the deposition of the spermatophore. Several of these sexual forms, and even males and females of the same species, have been described as new species in the past (Goto 1972*b*).

However, in the Symphypleona there are some species which exhibit very obvious differences between males and females (Betsch 1975*a*). Males of *Zebulonia massoudi* (Katianninae) from Madagascar have a strange glandular lump on the dorsal side of the body the function of which may be to produce pheromones to attract females (Betsch 1970). In some other Symphypleona, the male antennae are modified to form clasping organs which grasp the female during mating (Betsch 1967; Betsch and Massoud 1972; Fjellberg 1989). This feature is particularly conspicuous in the Subfamily Sminthuridinae (Massoud and Betsch 1970, 1972; Fig. 8.4).

8.3.3 Mating behaviour

The mating behaviour of Collembola covers a complete range from unsophisticated species in which the male apparently deposits his spermatophores throughout the environment for females to discover at random, to the other end of the scale where males and females indulge in an elaborate courtship before mating (Betsch 1974*c*; Bretfeld 1970, 1971; Hale 1965*a,b*; Klauer 1975). Females cannot retain sperm through an ecdysis so they need to collect a spermatophore after each moult if they are to continue to lay fertile eggs (Bretfeld 1977; Waldorf 1971*a*).

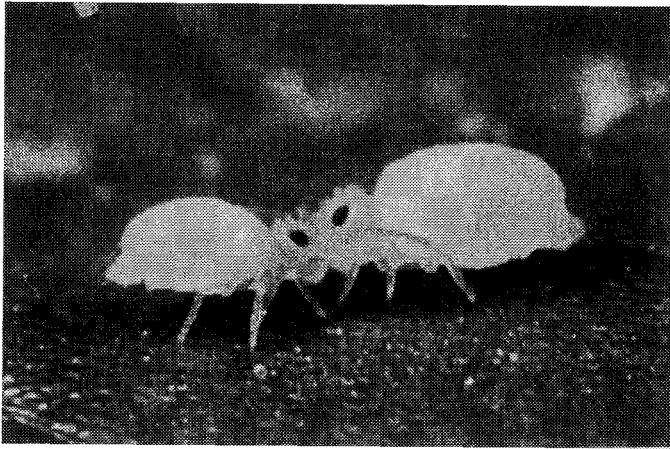


Fig. 8.5. 'Courting' pair of male (left) and female (right) *Bourletiella hortensis* (Sminthuridae) from Reading, UK. The female is approximately 1 mm in length. Photograph by Steve Hopkin.

One of the best accounts of such behaviour was the somewhat anthropomorphic, (but delightful) description made by Lubbock (1873). He wrote concerning '*Sminthurus luteus*' (= *Bourletiella hortensis*):

It is very amusing to see these little creatures coquetting together. The male, which is much smaller than the female, runs around her, and they butt one another standing face to face, and moving backwards and forwards like two playful lambs. Then the female pretends to run away and the male runs after her, with a queer appearance of anger; gets in front and stands facing her again; then she turns coyly round, but he, quicker and more active, scuttles round too, and seems to whip her with his antennae; then for a bit they stand face to face, play with their antennae, and seem to be all in all to one another.

Sitting in my garden in Reading more than 120 years later, I have observed this identical behaviour between the specimens of *Bourletiella hortensis* which cover the leaves of the plants during the spring and summer months (Fig. 8.5).

Within the Symphypleona, two main levels of mating behaviour have been recognised (Betsch-Pinot 1977). The simplest situation is where some primitive courtship occurs in species such as *Sminthurus viridis* and *Allacma gallica* (Fig. 8.6). The male lays down one or more spermatophores and the female takes up the spermatophore alone, sometimes with a little encouragement from the male. A more elaborate courtship is found in Sminthuridinae and some Bourletiellinae in which the males have modified antennae to clasp the female (Blancquaert 1981; Massoud and Betsch 1966c). In *Sphaeridia pumilis*, after some preliminary courtship, the male grabs the female antennae with his antennae and pulls her ventral surface towards his. He then transfers a drop of sperm to the female genital opening using his third pair of legs (Blancquaert and Mertens 1977). Copulation may last for more than 15 min during which the female may walk around and even

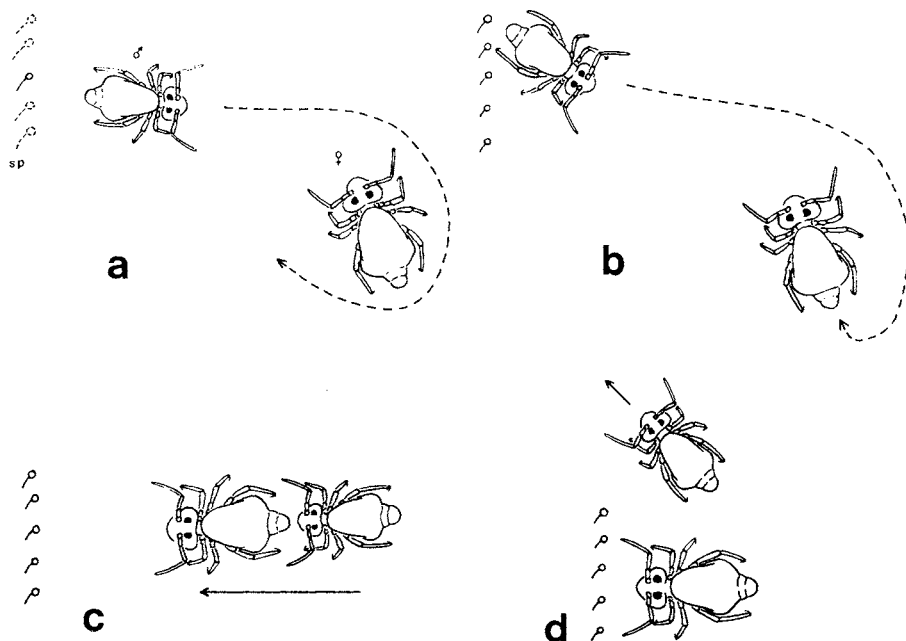


Fig. 8.6. Mating behaviour of *Allacma gallica* (Sminthuridae). (a,b) spermatophore deposition by male; (c) male guides female towards spermatophores; (d) female approaches spermatophores, male leaves. Reproduced from Betsch-Pinot (1977) by kind permission of the author and Editions Gauthier-Villars.

jump into the air (Hutasse-Jeannenot 1974). Similar behaviour has been observed in *Sminthurides aquaticus* which performs this ritual on the surface of the water. This explains why direct sperm transfer has evolved in this species as a spermatophore deposited directly on the water surface would be extremely vulnerable.

A number of other observations suggest that much remains to be discovered concerning reproductive behaviour of Collembola. For example, male *Orchesella cincta* eat the spermatophores of other males to reduce competition with their own (Hedlund *et al.* 1990). Pheromones are produced to facilitate aggregation of the sexes and hence increase the chances of successful collection by the females of male sperm (Joosse *et al.* 1973; Waldorf 1974b). In *Sinella curviseta*, the frequency of spermatophore deposition by males increases at the time of female moulting (Waldorf 1971a). This is one area of research where it is essential to watch living specimens in the laboratory rather than try to interpret reproductive behaviour from the morphology of dead specimens. Bretfeld has pioneered this approach and has made several films in which the mating behaviour of Bourletiellinae can be observed (Bretfeld 1973, 1974, 1976a,b).

8.3.4 Oviposition

The eggs are fertilised within the female before laying using stored sperm. Most species take about two to three minutes to lay an egg (Hale 1965a). Eggs may be

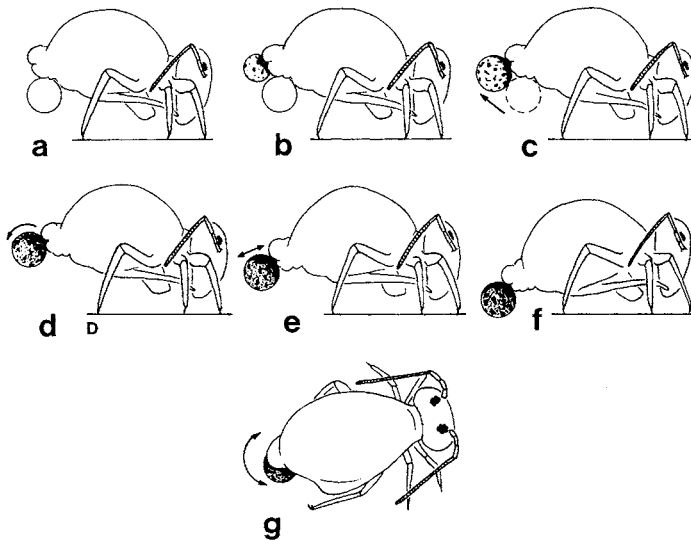


Fig. 8.7. Egg laying in *Sminthurus viridis* (Sminthuridae). (a) Release of egg from female genital opening; (b–e), coating of egg with fecal material; (f) deposition of egg on substrate; (g) further coating of egg with fecal material. Reproduced from Betsch-Pinot (1976) by kind permission of the author and Blackwell Wissenschafts-Verlag, Berlin.

laid individually or in small batches scattered throughout the soil or leaf litter (Sharma 1967), or on top of those already deposited by other females of the same species. Up to 10 000 eggs may accumulate in a single site in laboratory populations of *Proisotoma minuta* (Massoud and Betsch-Pinot 1974). The eggs of *Folsomia candida* in laboratory cultures accumulate in this way to form aggregates that can be seen easily with the naked eye.

Single eggs may be covered in a liquid suspension of faecal material extruded by the anus (Betsch-Pinot 1976; Bretfeld 1977; Fig. 8.7). The anal appendages, the structure of which is important in the taxonomy of Symphypleona, are involved in this coating process (Massoud and Pinot 1973). Clutches of eggs may be surrounded with fecal pellets which, when dry, provide a desiccation-resistant coating (Poinsoot 1970, 1971).

The fecundity of a single female depends on the number of eggs laid in each clutch, and the total number of clutches produced. In the laboratory, a female of *Sinella curviseta* with continuous access to a male, produces an average of 8 clutches with 50 eggs in each before she dies. Therefore her total fecundity is 400 eggs in a lifetime (Waldorf 1971a). Similar results have been found in *Willowsia jacobsoni* (Mari Mutt and Soto-Adames 1987) and *Sinella curviseta* (Niijima 1973; Waldorf 1971a).

Apart from effects due to temperature (Snider 1973), fecundity may also be affected by a number of other factors including crowding, food quality and presence or absence of males (Snider 1983a; Van Amelsvoort and Usher 1989a; Van Straalen 1985a; Waldorf 1971c). Since fecundity also depends on size, there is a trade off between reproduction and growth (Ernsting *et al.* 1993; Janssen *et al.*

1988). These are some of the reasons for the wide variation in values of fecundity for the same species quoted in the literature (Hale 1965*b*; see also Section 8.5)

Some species such as *Sinella curviseta* lay all their eggs in distinct clutches on a single occasion during an intermoult period whereas others such as *Sminthurides aquaticus* oviposit continuously when not moulting (Waldorf 1971*a*). Most species seem to alternate a feeding instar with an egg-laying instar (Ernsting *et al.* 1993; Joosse and Veltkamp 1970). In the laboratory, egg laying is sometimes observed to be synchronised within a population of the same species and this may be regulated by light, or the presence of males secreting pheromones which stimulate oviposition in the females at certain times (Chiba *et al.* 1973; Green 1964).

The egg may represent a 'dormant' or resistant stage in the life histories of Collembola (Leinaas and Bleken 1983). In the intertidal species *Anurida maritima*, for example, the adults all die in the Autumn and the population persists as eggs in diapause until the new generation emerges the following spring (Witteveen *et al.* 1988).

Once the eggs have been laid, they are subject to a wide range of predation pressures, not least by Collembola themselves (Petersen 1971*a*; Rapoport and Aguirre 1973; see also Sections 7.2.3 and 7.3.1). Thus there is a strong selective pressure to hide the eggs in crevices and make them as inconspicuous as possible.

8.4 Embryology

8.4.1 Normal embryonic development

One of the most detailed studies on embryonic development in Collembola was conducted on the Japanese species *Tomocerus ishibashii* by Uemiya and Ando (1987*a,b*, 1991) from which the following descriptions are taken (Figs. 8.8–8.13). Development can be divided into nine stages.

Stage 1

The egg is spherical and measures about 200 μm in diameter (Fig. 8.8). Blastodermic cuticle is produced under the chorion by blastodermic cells. Immediately prior to rupture of the chorion, the germ band is long and belt-like. The primary dorsal organ is situated between the anterior and posterior ends of the germ band. The dorsal organ is a peculiar structure which is initially a lens-shaped primordium but eventually develops a central region of columnar cells which send out very long apical processes. The exact function of the dorsal organ is not clear but it is probably involved in early cuticle formation and permeability (Tamarelle 1981). After rupture of the chorion, the newly-formed blastodermic cuticle becomes exposed to the air. This cuticle has four large curved spines (Fig. 8.8e). The two halves of the ruptured chorion come to lie at the bases of the two spines. The germ band eventually differentiates into the protocephalon and protocorm (Fig. 8.9a).

Stage 2 (Figs. 8.9b, 8.10a)

Segmentation of the embryo first becomes evident at this stage. Antennal, intercalary, mandibular, maxillary, labial and first thoracic segments are formed, and

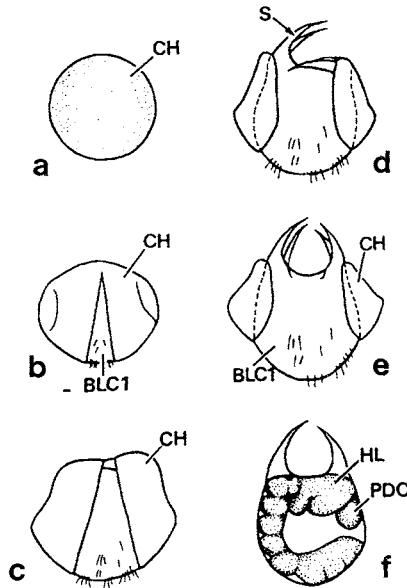


Fig. 8.8. Successive stages in egg development in *Tomocerus ishibashii* (Tomoceridae). BLC1, first blastodermic cuticle; CH, chorion; HL, head lobe; PDO, primary dorsal organ; S, spine. Reproduced from Uemiya and Ando (1987*b*) by kind permission of the authors and Elsevier Science.

the mediolongitudinal groove appears. The clypeolabrum (future labrum) forms anterior to the antennal segment and is not paired.

Stage 3 (Figs. 8.9c, 8.10b,c)

Segmentation of the abdomen begins and rudiments of the future thoracic legs develop. A rudimentary pair of second antennae are briefly visible on the intercalary segment (a possible 'throwback' to a crustacean ancestry?, see Section 3.2.1) but these quickly disappear, as in *Anurida maritima* (Tamarelle 1984).

Stage 4 (Figs. 8.9d,e,f, 8.11)

Blastokinesis begins and the thoracic segments, followed by the head and abdomen, sink into the yolk. The ventral sides of the head and abdomen come to face each other and the embryo retains this position until it hatches. The components of the mouthparts become further differentiated along with the thoracic legs. Six abdominal segments are formed and this number remains fixed for the remainder of the collembolan's life. Late in stage 4, rudiments of the appendages of the first, third and fourth abdominal segments appear.

Stage 5 (Figs. 8.9g, 8.12a,b,c)

The four primary segments of the antennae become distinct, the mouthparts differentiate further and the trochanter, femur and tibiotarsus of the legs can be recognised. Rudiments of the ventral tube and tenaculum enlarge on the first and third

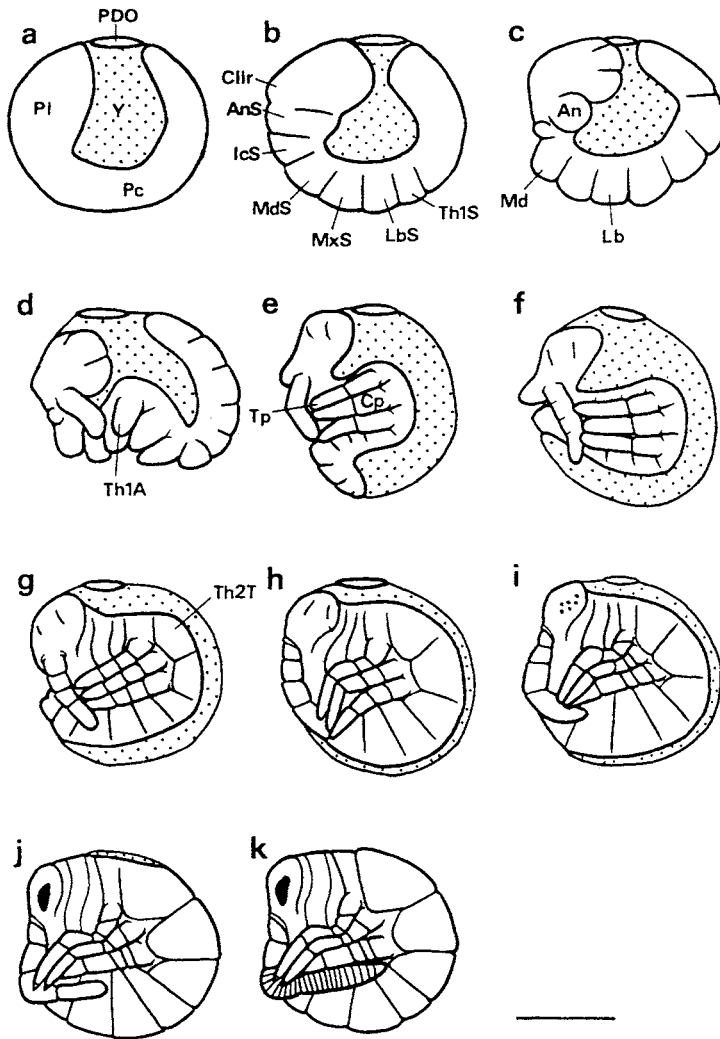


Fig. 8.9. Lateral views of embryonic development of *Tomocerus ishibashii* (Tomoceridae) with chorion and blastodermic cuticle omitted. (a) stage 1, (b) stage 2, (c) stage 3, (d) early stage 4, (e) middle stage 4, (f) late stage 4, (g) stage 5, (h) stage 6, (i) stage 7, (j) stage 8, (k) stage 9. Scale bar = 100 μm . For abbreviations, see Fig. 8.10. Reproduced from Uemiya and Ando (1987a) by kind permission of the authors and Alan R. Liss.

abdominal segments respectively, and the dens, mucro, and as yet unfused manubrium of the future furca, are clearly visible.

Stage 6 (Figs. 8.9h, 8.12d,e,f)

Further development of the mouthparts takes place and the first and second pairs of legs become S-shaped. The dorsal region of the first thoracic segment begins to

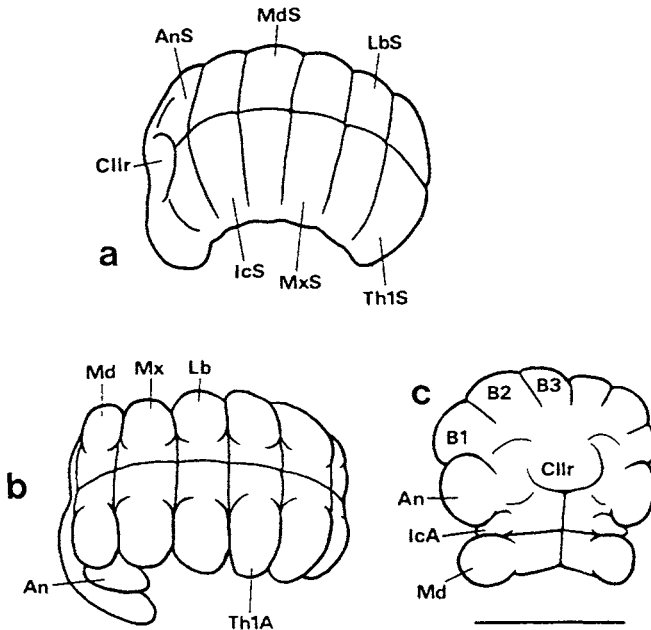


Fig. 8.10. External features of embryos of *Tomocerus ishibashii* (Tomoceridae). (a) Ventrolateral view stage 2, (b) ventrolateral view stage 3, (c) frontal view of head stage 3. Scale bar = 100 μ m. I–VI, first to sixth abdominal segments; Ab1–4A, first to fourth abdominal appendages; An, antenna; AnS, antennal segment; B1–3, protocephalic bulges 1–3; BP, basal plate; Cllr, clypeolabrum; Cp, coxopodite; Cr, corpus; Cy, cylinder; De, dens; Fu, furca; Ga, galea; Gl, glossa; IcA, intercalary appendage; IcS, intercalary segment; In, incisor; La, lacina; Lb, labium; LbP, labial palp; LbS, labial segment; LbSu, labial suture; LbT, labial tergum; Li, lingua; Lr, labrum; Ma, manubrium; Md, mandible; MdS, mandibular segment; MdT, mandibular tergum; Mo, molar; Mu, mucro; Mx, maxilla; MxP, maxillary palp; MxS, maxillary segment; MxT, maxillary tergum; Oc, ocellus; Pc, protocorm; PDO, primary dorsal organ; Pgl, paraglossa; Pl, protocephalon; Pm, postmentum; Ra, ramus; S, labial sternum; Sba, subanal lobe; Sli, superlingua; Spa, supraanal lobe; SR, sclerotised region; Te, tenaculum; Th1A, first thoracic appendage; Th1S, first thoracic segment; Th2T, second thoracic tergum; Tp, telopodite; TV or V, ventral tube; Y, yolk. Reproduced from Uemiyama and Ando (1987a) by kind permission of the authors and Alan R. Liss.

develop at a slower rate than thoracic segments two and three and becomes narrower and much less sclerotised, one of the characteristic features of Entomobryomorpha. The appendages on the abdomen meet on the mid-ventral line and the terminal vesicles of the ventral tube become visible.

Stage 7 (Figs. 8.9i, 8.13a,b,c,d)

As dorsal closure advances, the superficial region of the primary dorsal organ shrinks. Six ocelli appear as blue-black dots on each side of the head, the same as in the adult. The mouthparts are gradually enclosed by downgrowth of the tergites of the gnathal segments so only their tips are visible externally, the entognathous condition. Further differentiation of the legs and abdominal appendages takes place.

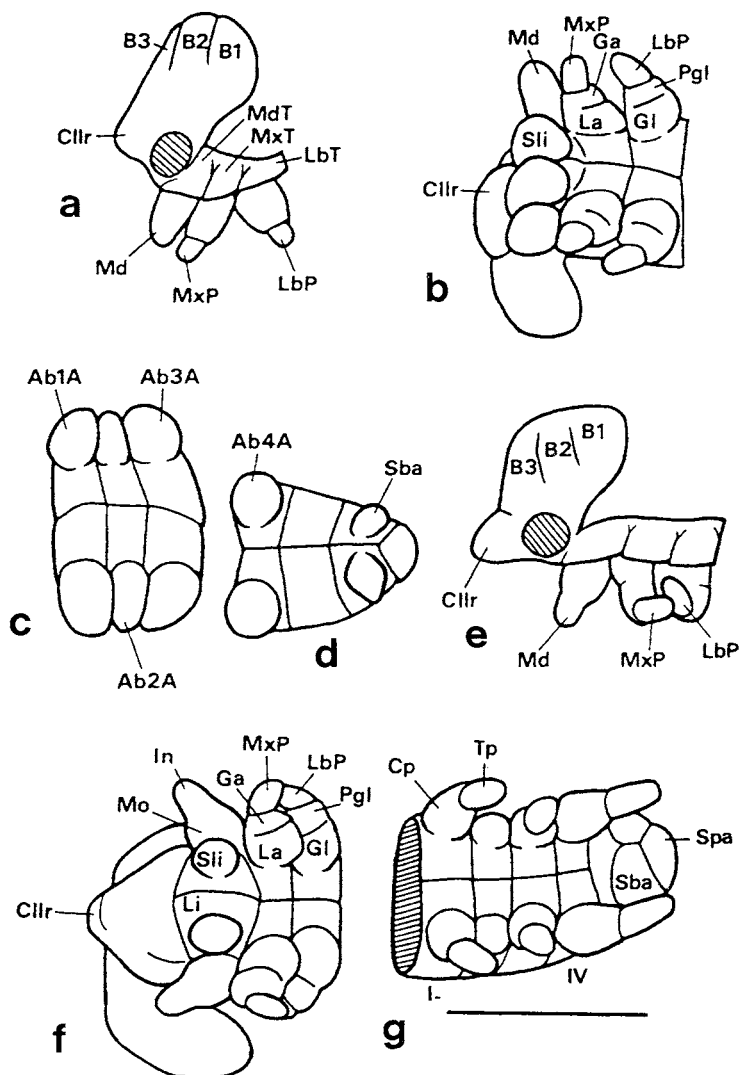


Fig. 8.11. External features of embryos of *Tomocerus ishibashii* (Tomoceridae). (a) Lateral view of head middle stage 4 with antenna removed, (b) ventrolateral view of head middle stage 4, (c) ventrolateral view of first three abdominal segments middle stage 4, (d) ventrolateral view of fourth to sixth abdominal segments middle stage 4, (e) lateral view of head late stage 4 with antenna removed, (f) ventrolateral view of head late stage 4, (g) ventrolateral view of abdomen late stage 4. Scale bar = 100 μ m. For abbreviations, see Fig. 8.10. Reproduced from Uemiyama and Ando (1987a) by kind permission of the authors and Alan R. Liss.

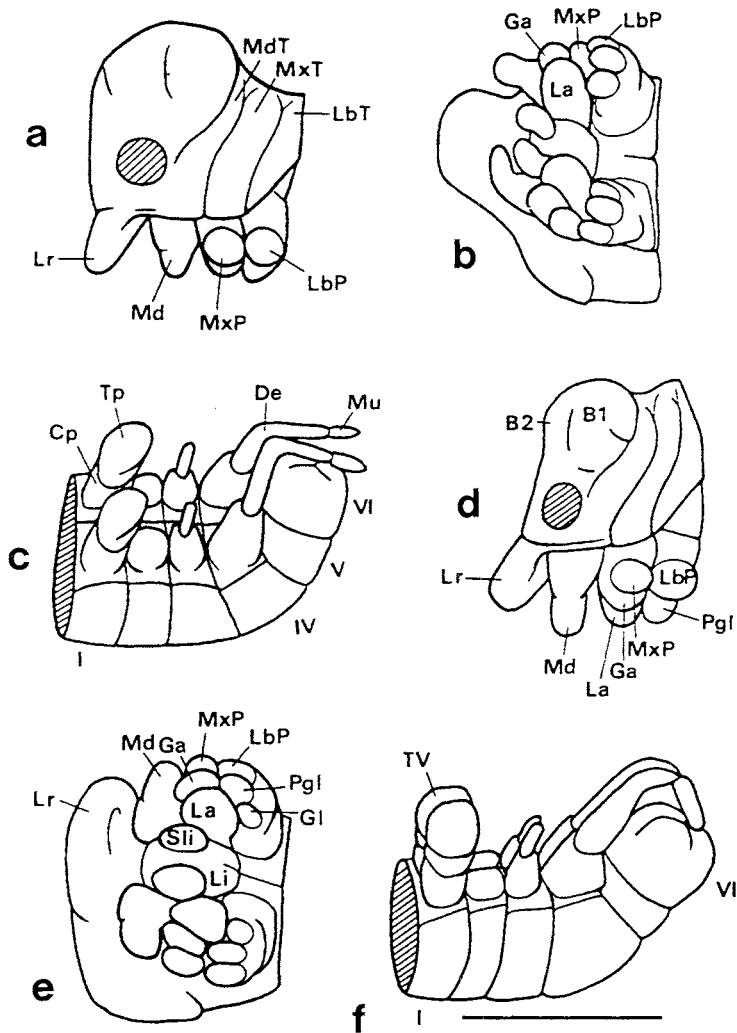


Fig. 8.12. External features of embryos of *Tomocerus ishibashii* (Tomoceridae). (a) Lateral view of head stage 5 with antenna removed, (b) ventrolateral view of head stage 5, (c) ventrolateral view of abdomen stage 5, (d) lateral view of head stage 6 with antenna removed, (e) ventrolateral view of head stage 6, (f) ventrolateral view of abdomen stage 6. Scale bar = 100 μ m. For abbreviations, see Fig. 8.10. Reproduced from Uemiyu and Ando (1987a) by kind permission of the authors and Alan R. Liss.

Stage 8 (Figs. 8.9j, 8.13e)

Dorsal closure is complete except for the labial to second thoracic segments. The primary dorsal organ is no longer visible on the surface of the embryo and it eventually passes into the alimentary canal and is digested. The final structure of

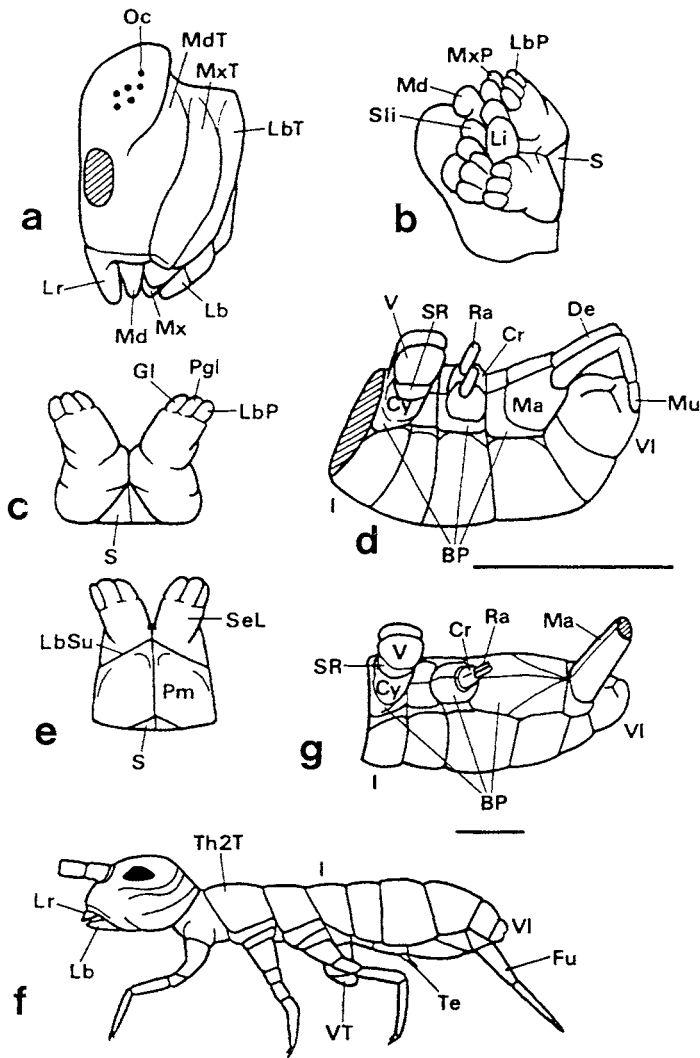


Fig. 8.13. External features of embryos (a–e) and first instar (f,g) of *Tomocerus ishibashii* (Tomoceridae). (a) lateral view of head stage 7 with antenna removed, (b) ventrolateral view of head stage 7, (c) posterior view of labium stage 7, (d) ventrolateral view of abdomen stage 7, (e) posterior view of labium stage 8, (f) lateral view with third and fourth antennal segments removed, (g) ventrolateral view of abdomen with dens and mucro removed. Scale bars = 100 μ m. For abbreviations, see Fig. 8.10. Reproduced from Uemiya and Ando (1987a) by kind permission of the authors and Alan R. Liss.

mouthparts nears completion. At the tips of the legs, claws develop comprised of the primary claw and opposing empodium.

Stage 9 (Fig. 8.9k)

Dorsal closure is completed and final development occurs. The third and fourth segments of the antennae develop annulations and the fourth ones elongate. The

posterior part of the head forms from dorsal parts of the three gnathal segments which extend dorsally. The first instar juvenile (Fig. 8.13f,g) hatches from the egg and begins its development towards the adult stage (Section 8.5). Aspects of posthatching development in another species in the same genus (*Tomocerus minutus*) have been studied by Uchida and Chiba (1958, 1959) and Uchida and Hongo (1962).

Development of the embryo of *T. ishibashii* takes about 10 days at room temperature. In epedaphic or hemiedaphic species such as *Orchesella cincta* and *Tomocerus minor* (Mertens and Blancquert 1980; Van Straalen and Joosse 1985), or *Entomobrya aino* (Hisamatsu *et al.* 1986), there is an approximately linear relationship between egg development rate and temperature, although the slopes differ between species (Fig. 8.14). In *Entomobrya nivalis*, egg development takes 25 days at 9°C, 15 days at 13°C, and only 7 days at 20°C (Von Allmen and Zettel 1982, 1983).

Embryological development of other species of Collembola is similar to that of *T. ishibashii* (see e.g. Bruckmoser 1965; Thibaud 1968a). The large onychiurid *Tetradontophora bielensis* (up to 10 mm in length) is particularly suitable for such work and most aspects of its early development have been described (Fryc 1971; Jura 1965, 1966, 1967a,b, 1972; Jura and Krzystofowicz 1977, 1982, 1986, 1992; Klag 1982a,b, 1983a,b, 1984; Klag and Ksiazkiewicz-Kapralska 1989, 1990; Klag and Witalis 1990; Krzystofowicz 1967b, 1986a,b; Tyszkiewicz 1976; Witalis 1993).

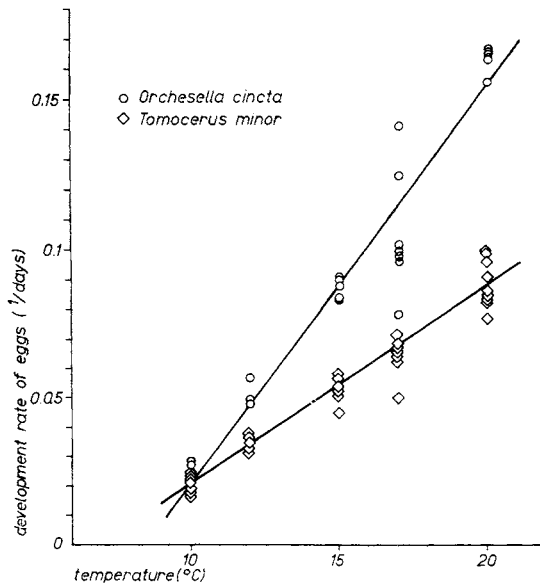


Fig. 8.14. Development rate of eggs (reciprocal of duration) as a function of temperature for *Orchesella cincta* (Entomobryidae) and *Tomocerus minor* (Tomoceridae). Each point gives a value for an individual clutch. Straight lines are based on regression analysis. Reproduced from Van Straalen and Joosse (1985) by kind permission of the authors and Gustav Fischer.

8.4.2 Abnormal development

Arthropod development is under the control of clusters of *Hox* genes which regulate large numbers of other genes (Section 3.2.1). Apart from developmental abnormalities due to physical damage, two things can go wrong at the embryological stage. First the *Hox* genes can induce development of (or fail to suppress) a structure on a segment on which it would not normally appear. For example, Fjellberg 1976*b* reported the presence in *Proisotoma subarctica* of an extra tenaculum on abdominal segment 2 in addition to the normal tenaculum on abdominal segment 3 (Fig. 8.15). Second, an appendage may develop in the correct position, but in an atypical way (Dallai 1971*b*; Najt and Massoud 1976; Fig. 8.16). 'Freaks of nature' might be thought to be curios not worthy of scientific investigation. However, the existence of such deformities may provide important information for elucidating developmental processes. Specimens exhibiting abnormal features should be carefully preserved and their morphology described and published.

8.5 Postembryonic development and life histories

Juvenile Collembola begin feeding soon after emergence from the egg. Apart from their lack of functional reproductive organs, absence of secondary sexual characters, and differences in their chaetotaxy, they resemble their parents (Barra 1975*a,b*; Korr 1968; Rusek 1980*b*; Snider 1977). Growth is rapid as they pass through a number of instars or *stases*, each with a characteristic morphology before they become adult (André 1986, 1987, 1989*b*, 1991; Gregoire-Wibo 1974;

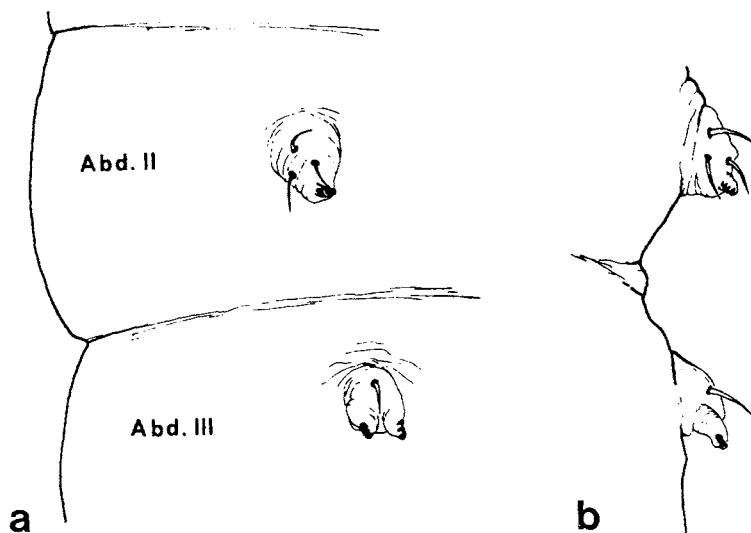


Fig. 8.15. Ventral (a) and lateral (b) views of second (Abd. II) and third (Abd. III) abdominal segments of an abnormal specimen of *Proisotoma subarctica* (Isotomidae) with an extra tenaculum-like structure on Abd. II. Reproduced from Fjellberg (1976*b*) by kind permission of the author and Editions Gauthier-Villars.

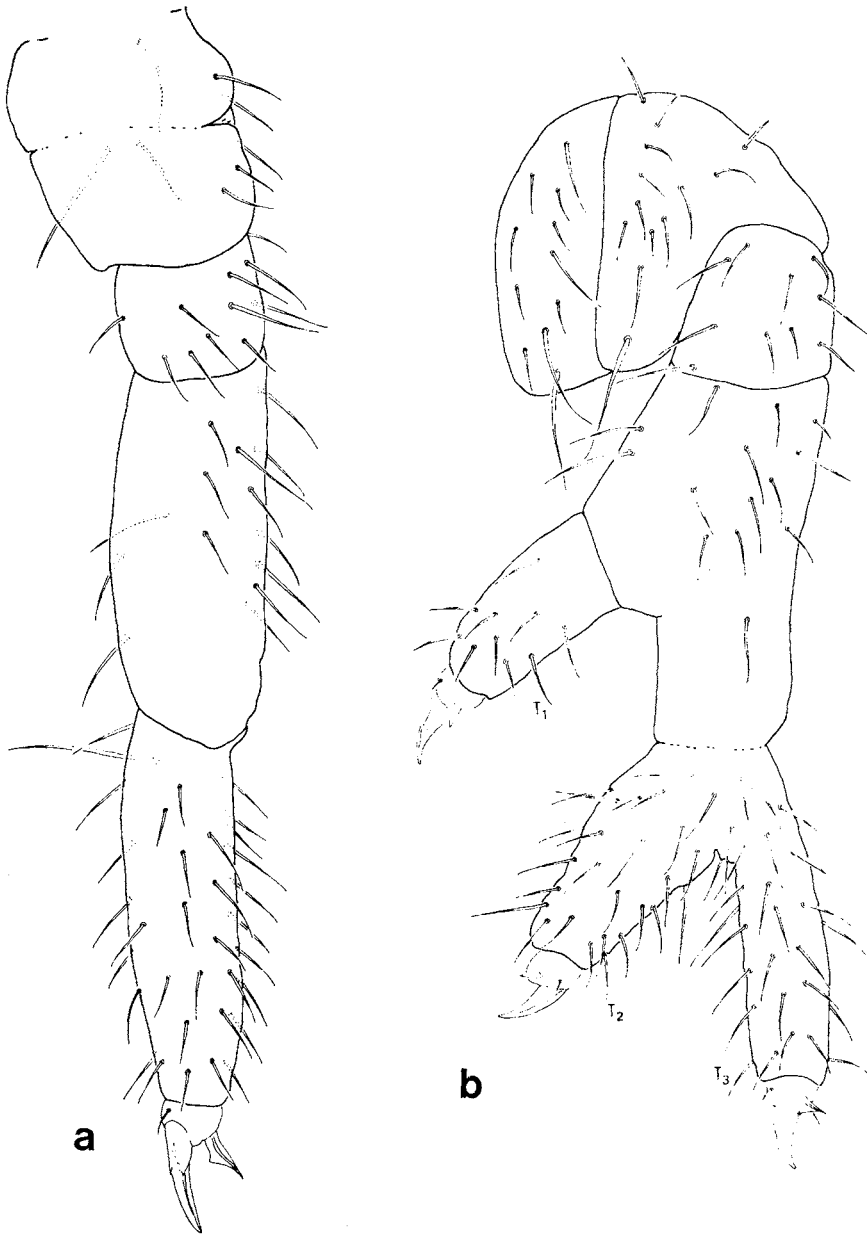


Fig. 8.16. Normal (a) and abnormal (b) third leg of *Isotomurus palustris* (Isotomidae). Reproduced from Najt and Massoud (1976) by kind permission of the authors and Editions Gauthier-Villars (b after Dallai 1971b).

Thibaud 1980a; Weiner 1989a). The number of instars before reproductive maturity is reached is typically about 5–8 although in the euedaphic *Mesaphorura krausberi* it is as few as 3 (Hale 1965c) and in *Orchesella cincta* 11–13 (Janssen and Joosse 1987). Springtails are at their most vulnerable during this period as predation pressure in the field is higher during the first few stases than in the egg or adult stages (Van Straalen 1985b).

On attaining maturity, the adults continue to moult, in some species as many as 40 times or more (Mari Mutt and Soto-Adames 1987), each successive stage being known as an *instar* (Mertens *et al.* 1982; Petersen 1971c). Unless the collembolan enters an ecomorphic, epitokous or cyclomorphic stage (Section 8.6), the morphology of these adult instars is essentially similar. The duration of the intermoult period increases with age. Thus in *Heteromurus nitidus* (at 20°C) the average intermoult period is 4.3 days for juvenile instars 1–6, 6.5 days for adult instars 7–9, 8.2 days for instars 10–16, and 9.5 days for instars 17–31, after which most of the animals die (Krool and Bauer 1987).

A very large number of papers have been published on the life history characteristics of different species of Collembola (too many to review in detail here). The main characteristics which vary between species are longevity, number and duration of juvenile and adult instars, fecundity (number of eggs laid per clutch and number of clutches laid by individual females) and rate of spermatophore production. All of these factors are influenced by availability and quality of food, and temperature (Joosse and Testerink 1977; Joosse *et al.* 1973; Kojima 1985; Marques *et al.* 1987; Mertens and Blancquaert 1980; Mertens *et al.* 1983; Nijima 1975; Seifert *et al.* 1981; Thibaud 1968b; Thibaud and Oliveira 1988). There are also trade-offs between energy used for respiration, growth and reproduction (Ernsting *et al.* 1993; Testerink 1982; Van Straalen 1983), and exposure to predators. For example, *Orchesella cincta* has a more superficial and active way of life and is more responsive to temperature than *Tomocerus minor* in coniferous woodlands in The Netherlands (Fig. 8.14). This increases *O. cincta*'s chances of being preyed upon, but allows more effective reproduction than in *T. minor* (Joosse 1981; Van Straalen 1985a, 1989).

The maximum authenticated longevity for a springtail in the laboratory is 5 years 7 months in *Pseudosinella impediens* (Barra 1976). However, it is possible that individuals of some species may live for much longer in the wild, particularly in stable cave environments (Thibaud 1976b; see also Section 10.2). In very cold climates, growth and reproduction occur at much slower rates. Thus in the Antarctic, the complete life cycle (egg to egg) of *Cryptopygus antarcticus* takes a minimum of 2 years and individuals of this species may possibly live for more than 7 years (Burn 1981; Convey 1994). Populations of Antarctic springtails comprise many overlapping generations (Sømme 1986a).

Tropical epedaphic species may have very short intermoult periods, for example only 3.8 days in the Malaysian *Callyntrura chibai* (Paronellidae) at 26°C (Chiba 1976). The record for length of intermoult period of 110 days at 9.5°C is held by the Korean species *Gulgastrura reticulosa* (Lee and Thibaud 1987).

Some species are univoltine (one generation per year) while others are multivoltine (more than one generation per year). Hisamatsu and Matsunaga (1994) com-

pared the life cycles of examples of each of these types in a Japanese red pine (*Pinus densiflora*) forest on the slopes of Mount Fuji. *Tomocerus cuspidatus* is univoltine with a synchronised short breeding period in the spring. Eggs laid in the litter layer in April hatch in May. The juveniles subsequently climb the trunks in June and mature on the trees by November. Overwintered adults descend into the litter in March and lay their eggs there in April. In contrast, *Entomobrya aino* is multivoltine. This species overwinters as eggs which hatch in the spring allowing at least two subsequent generations before the following winter.

8.6 Ecomorphosis, epitoky and cyclomorphosis

Some species of adult Collembola, mainly in the families Hypogastruridae and Isotomidae, may go through one or more stages in their life cycle characterised by reduced activity and respiration and distinct morphology (Bourgeois 1973, 1982; Cassagnau and Ferrero 1966; Cassagnau and Raynal 1964; Culik and Najt 1986; Fjellberg 1977a; Takeda 1985). Studies on ecomorphosis were pioneered by Cassagnau and co-workers (reviewed by Cassagnau 1986b,c, 1990a). These phenomena were referred to collectively as 'ecomorphosis' by earlier authors although most modern workers now recognise three main types namely ecomorphosis, epitoky and cyclomorphosis.

Ecomorphosis (*sensu stricto*) is now reserved for phenomena induced by specific climatic conditions (Raynal 1974, 1976). This stage is characterised by a number of morphological changes (see below) and cessation of feeding, and is an adaptation to extreme climatic conditions, mainly high temperature and low humidity (Cassagnau 1974a). Ecomorphosis can be induced in laboratory populations of *Hypogastrura boldorii* by raising the temperature (called an 'ecomorphic crisis' by Bedos and Cassagnau 1988). Where the stage is part of a reproductive cycle it is known as *epitoky* (Cassagnau 1985; Cassagnau and Lauga-Reyrel 1992; Fjellberg 1988c,d; Waltz and Hart 1987). Development of a morphologically distinct stage as part of a regular seasonal cycle is called *cyclomorphosis* (Fjellberg 1976a, 1978b; Leinaas 1981b,c; Waltz and Hart 1995a; Zettel and Zettel 1986, 1989). In *Isotoma hiemalis* the appearances of the summer and winter forms are controlled by an endogenous 'clock' which 'counts the days' until cyclomorphosis takes place (Zettel 1985).

Ecomorphosis, epitoky and cyclomorphosis are not mutually exclusive and in certain circumstances it may be difficult to attribute changes in adult morphology to one of these causes alone. Their initiation and cessation are probably controlled by hormones released by the neurosecretory system (Lauga-Reyrel 1984a,b).

Features characteristic of ecomorphosis in its widest sense include changes in the morphology of the chaetotaxy, shape of the mucro and mouthparts, loss of secondary sexual characteristics, presence of large spines on the posterior of the abdomen and internal modifications such as atrophy of the digestive tract, alterations in the appearance of the gonads, and accumulation of fat and excretory granules (Bannon and Engstrom 1980; Cassagnau and Dalens 1976; Cassagnau and Fabres 1968; Lauga-Reyrel 1979, 1980, 1981, 1984d; Lucianez and Simon

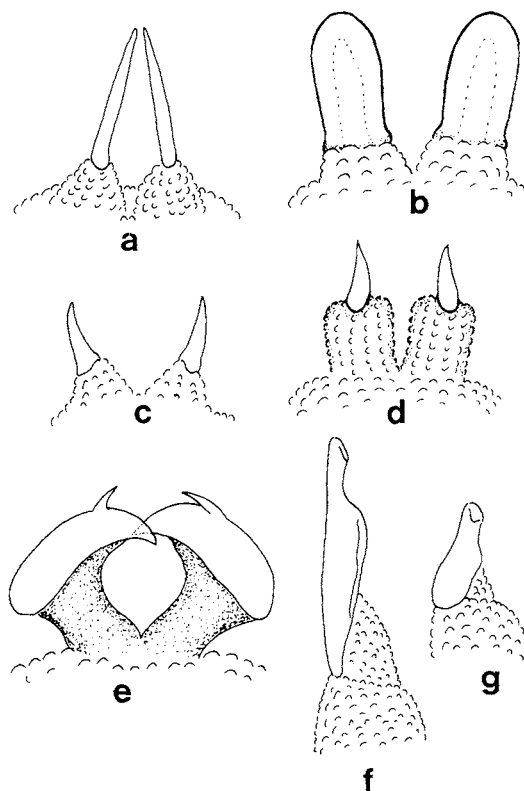


Fig. 8.17. Anal spines of *Ceratophysella armata* (Hypogastruridae) (a) form A, (b) form B (formerly described as *C. crassispina*). Anal spines of *Hypogastrura purpureescens* (Hypogastruridae) (c) form A, (d) form B, (e) form C (formerly described as *Ancistracanthella*). Mucro viewed in profile of *Hypogastrura boldorii* (f) form A, (g) form C. Reproduced from Cassagnau (1986b) by kind permission of the author and Société Entomologique de France.

1992c; Miles 1994; Figs. 8.17, 8.18). The granules on the surface of the cuticle may also become much closer together and this has been interpreted as an adaptation to reduce transpiration under dry conditions (Dalens and Vannier 1979; Lauga-Reyrel 1984c; Najt 1983). Although there is a common pattern to these modifications, their intensity varies between species, and even within the same species from one population to another (Bourgeois 1974).

Ceratophysella sigillata passes through two of these stages during its life cycle and has four different morphs, A (active), B (active, transition to C), C (cyclomorphosis) and E (epitoky) (Table 8.1). In forests in Switzerland the species appears as juveniles in the spring, undergoes an inactive cyclomorphic summer dormancy and enters epitoky when it reproduces in the spring of the second year (Zettel and Zettel 1994b). *C. sigillata* are found at the surface in huge aggregations of several centimetres in thickness and these colonies migrate by jumping for distances of

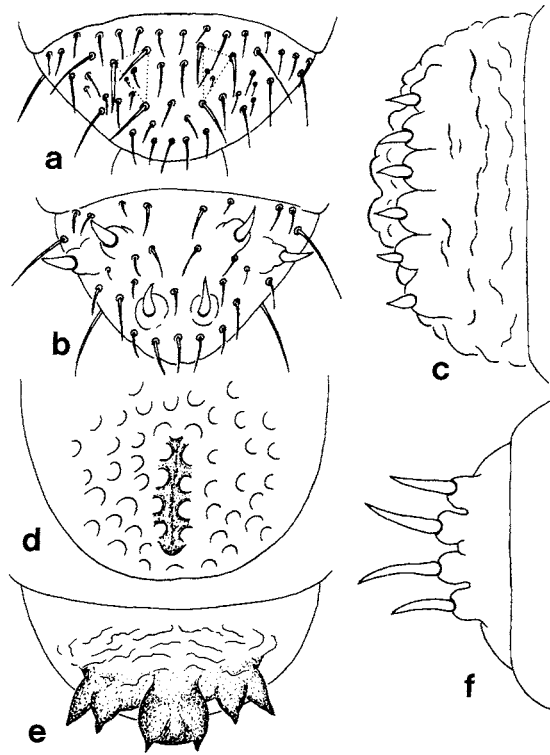


Fig. 8.18. Spines and other structures on the posterior abdominal segments of Isotomidae. *Cliforga alleghaniensis* (a) form A, (b) form B. (c) *Desoria graeca* form B. (d) Median cleft in last abdominal segment of *Folsomia nigromaculata* (Isotomidae) form B. (e) *Desoria tigrina* form B. (f) *Isotoma viridis* form B. Reproduced from Cassagnau (1986b) by kind permission of the author and Société Entomologique de France.

Table 8.1. Succession of morphs during ontogeny of *Ceratophysella sigillata* (Hypogastruridae) in a mixed forest 10 km north of Berne, Switzerland at an altitude of 640 m above sea level (see text for further details). Reproduced from Zettel and Zettel (1994b) by kind permission of the authors and the Finnish Zoological and Botanical Publishing Board

Year 1						
Month	May	June	June	November	February	March
Instar	1	2	3	4	5	6
Morph	A	A	C	A	A	E
Year 2						
Month	April	April	May	November	February	March
Instar	7	8	9	10	11	12
Morph	B	B	C	A	A	E
Year 3						
Month	April	April	May			
Instar	13	14	15			
Morph	B	B	C	?		

30–50 cm per hour. This generates a rustling noise which can be heard at a distance of several metres.

The mucro of forms A and B is large and boat-shaped and the antennae bear a protrudable vesicle between segments 3 and 4. A and B morphs enter ecomorphosis in the spring when they moult into inactive C morphs; these form dense clusters deep in the leaf litter, and remain motionless for 4–5 months. According to Zettel and Zettel (1994b), ‘they have a striking resemblance to a flock of sheep’. These C morphs moult back into A morphs for the winter, eventually developing into reproductive E morphs in April/May of their second year when they enter epitoky. The E morph lasts for about 3 weeks and is quite active, crawling over the surface but not using the furca to jump. About 50% live beyond epitoky to reproduce for a second year but very few animals survive into a third year of life (Zettel and Zettel 1994a).

There are numerous examples in the literature of new species or even genera being described which have been shown subsequently to be ecomorphic forms of existing taxa. For example *Spinisotoma*, an apparently new genus of isotomid with characteristic spines on the posterior margin of its abdomen, was shown subsequently to be an ecomorphic form of *Isotoma* (Stach 1961). Careful study is required to determine whether apparently new species are true biological species and not simply existing taxa undergoing epitoky, cyclomorphosis or ecomorphosis (Cassagnau and Izarra 1969; Fjellberg 1976d, 1978a; Najt *et al.* 1984).

8.7 Parthenogenesis and sex ratios

Parthenogenesis occurs when females lay unfertilised eggs which develop into viable offspring. Males are completely absent from purely parthenogenetic populations. Petersen (1980) considered that the majority of parthenogenetic springtails were euedaphic. There are two ways in which parthenogenesis can be demonstrated. First, by showing that field populations of certain species exist only as females. Second, by maintaining female only populations of a species in the laboratory for several generations.

In his detailed study of the Collembola of a Danish beechwood, Petersen (1980) could find no males of *Willemia anophthalma*, *Paratullbergia callipygos*, *Mesaphorura krausberi*, *M. macrochaeta*, *M. sylvatica*, *Isotomiella minor*, *Isotoma notabilis*, and *Megalothorax minimus*. Populations of eight additional but less abundant species also lacked males and it was concluded that parthenogenetic Collembola comprised about 72% of the mean annual number of springtails in the forest soil. Female-only populations have also been found of *Papirinus prodigiosus* (Sminthurinae) in forests on the slopes of Mount Fuji, Japan (Itoh *et al.* 1985), and *Proisotoma oliveirae* from Brasil (Deharveng 1984a).

The most well-known parthenogenetic species is *Folsomia candida* (see Fig. 10.1) which is maintained in culture in numerous laboratories throughout the world (Green 1964; Snider 1973). The ease with which *F. candida* can be bred, and its short reproductive cycle, has led to its designation as the ‘standard’ springtail for ecotoxicological testing (see Section 10.2). In my laboratory, we have

selected genetically homogenous 'Reading strains' of *F. candida* by starting new cultures from single unfertilised females kindly donated to us from populations held at the University of Southampton.

The ease with which *F. candida* can be bred has allowed strains to be selected which are resistant to certain chemicals (Grimnes 1986). Other species which reproduce without males in the laboratory include *Protaphorura yolandae* (Rapoport and Aguirre 1973) and *P. hortensis* (Goto 1960; Pomorski 1989).

However, many parthenogenetic species also exist in non-parthenogenetic forms. Although Petersen (1971*b*) demonstrated that *I. notabilis* and *M. krausberi* were parthenogenetic in the laboratory, Hutson (1978*b*) was able to show that they could both exist in sexually reproducing populations as well. Most populations of *Neanura muscorum* in south west France are parthenogenetic and polyploid (females with tetra-, tri-, penta, and hexaploidy can be found). Nevertheless, there are some isolated populations in which males are present and normal sexual reproduction occurs (Cassagnau 1972*b*). Sexual and parthenogenetic reproduction has also been found in *Mesaphorura italica* in Spain (Mateos 1992) and *M. clavata* in Indiana, USA (Waltz and Hart 1995*b*).

The factors which control the ratio of males to females in Collembola are not absolutely clear but the sex ratio is probably related at least partially to climate. Choudhuri (1961) maintained that populations of *Onychiurus imperfectus* had more males than females if eggs were reared at 20°C or above, whereas at 14°C or below, there were more females than males. Under certain environmental conditions, parthenogenicity may be selectively advantageous in allowing the population of a species to increase its numbers more rapidly than would be possible with sexual reproduction. However, the mechanisms behind this phenomenon are not fully understood.

Ecology and conservation

9.1 Introduction

Earlier sections of this book have covered interactions of Collembola with their abiotic and biotic environments. In this Chapter, the distribution of different species on the local through to global scale is examined. Following a discussion of observation and sampling techniques (Section 9.2), the distribution of springtails in space and time is reviewed (Section 9.3). Critically examined are the proposals that presence or absence of certain species of Collembola, or characteristic assemblages of species, can be used to indicate properties of habitats that would otherwise be difficult to elucidate (Section 9.4). Conservation of Collembola is discussed (Section 9.5) and the Chapter ends with a short review of the biology and distribution of Collembola that occur in caves (Section 9.6).

9.2 Observation and sampling techniques

There are three main ways in which the distribution of Collembola can be studied on a local scale. These are

- direct observation of live individuals in their natural environment
- trapping the animals for subsequent examination in the laboratory
- collecting soil and leaf litter and extracting the springtails from it (Edwards 1991; Eisenbeis 1994).

Collembola are small animals and are difficult to study in the field in comparison to larger insects such as bugs, butterflies and beetles. However, much useful information can be obtained by simply turning over stones and rotting wood, spreading leaf litter on a plastic sheet in the field and collecting the springtails that try to hop away, or examining trees, above-ground vegetation and the surfaces of ponds, puddles and streams. It is not long before one is able to predict which species are likely to be found in particular habitats. In England for example, *Podura aquatica* is invariably present on the surfaces of puddles, *Entomobrya nivalis* on the bark of trees, *Neanura muscorum* under rotting wood and *Anurida maritima* on the seashore.

Specimens are usually preserved in a mixture of seven parts ethanol to three parts water ('70% alcohol'). However, it is worth taking the time to watch live springtails so that their beautiful colours (which fade in preservative) can be appreciated. In addition, many aspects of collembolan behaviour can be observed

directly by those with a keen eye and a little patience (see for example, Figs. 8.5–8.7). Rhizotrons with glass panels held vertically against the soil profile allow the distribution and behaviour of Collembola to be studied directly in semi-field conditions in this otherwise inaccessible habitat (Gunn and Cherrett 1993; Wilson *et al.* 1995) and to be recorded with video cameras (Lussenhop and Fogel 1995; Lussenhop *et al.* 1991; Snider *et al.* 1990).

Enclosures have been employed in ecological studies where springtails are excluded from, or retained within, a portion of habitat (Faber and Verhoef 1991; Kennedy 1994). Such enclosures have included porous bags of different mesh diameter in which leaf litter is retained. The bags can be defaunated by application of naphthalene (Best *et al.* 1978) or gamma radiation (Coleman and Macfadyen 1966), or the litter can be treated to attract or repel Collembola (Scholle *et al.* 1995). Subsequent recolonisation is then monitored (Argyropoulou *et al.* 1993; Hasegawa and Takeda 1995; Malatesta *et al.* 1986; Reddy and Alfred 1989b).

Collembola may be trapped in the field using a wide variety of methods, including the litter bag technique described above (Gunadi 1994). Vacuum sampling is very efficient but it is hard work to sort the springtails from the seeds, soil particles and other invertebrates which get sucked up too (Purvis and Curry 1980). Sticky traps are messy but are an effective way of monitoring activity (Schenker and Block 1986), particularly up and down trees (Bowden *et al.* 1976; Itoh 1991).

Pitfall traps have been employed frequently to collect surface-active species (Joosse 1965; Joosse and Kapteijn 1968; Snider and Calandrino 1987). The trap is sunk into the ground so that its rim is level with the soil surface and it is filled with preservative, usually ethylene glycol to which a tiny amount of detergent is added to make the Collembola sink. The traps are left for periods of a day to several months, after which the contents can be returned to the laboratory for sorting (Berbiers *et al.* 1989). Other traps have included bark boxes on trees for trapping epedaphic species (Elbourne 1970). In caves, baits have been laid to attract Collembola which might otherwise never be seen (Christiansen 1970a).

A recently developed sampling method is canopy fogging. Wide-mouthed funnel traps are positioned beneath trees and clouds of non-persistent insecticide are released into the foliage (Hijii 1989). The invertebrates that are killed fall from the branches into the traps (Greenslade and Sutrisno 1994). Use of this technique has highlighted the hitherto unsuspected diversity of the springtail fauna of forest canopies, particularly in the tropics (Guilbert *et al.* 1995; Palacios-Vargas and Gonzalez 1995; Stork 1988). Lee and Park (1984) discovered a new species *Entomobrya monopunctata* in Korea which was extracted from pine cones using insecticides.

Collembola which are very small (<1 mm in length), and which crawl into inaccessible spaces in soil and leaf litter, can be captured *en masse* by bringing their habitat into the laboratory. If a soil sample is frozen in the field, the exact distribution of the springtails can be determined by cutting thin sections (Babel and Vogel 1989; Rusek 1975a, 1985a). However, if all the specimens are required from the soil, conditions must be created which induce the springtails to leave the sample. The most common extraction technique is to place the soil or leaf litter on a wire

or plastic mesh in a 'Tullgren funnel' (named after the famous soil zoologist who is credited with its invention) and to heat the sample from above using an electric light bulb. As the material in the funnel slowly dries out, the animals move down the profile to the moister layers until eventually they fall through the mesh into a container of preservative below. In dense soil, complete extraction may take more than a week.

Numerous papers have been published on the legitimacy of the Tullgren funnel technique and many modifications have been proposed (Huhta *et al.* 1986; Itoh *et al.* 1985; Lasebikan 1971; Takeda 1979b). If one accepts that extraction will not be 100% efficient (in my experience in trials where known numbers of *Folsomia candida* were added to Tullgren funnels containing defaunated field soils it averages 85%), then this very simple technique is an acceptable method for quantifying soil and leaf litter populations of springtails. Tullgren funnels can also be used in the field using the sun as an overhead source of heat (Deharveng *et al.* 1989; Lawrence, personal communication).

Another method of extraction takes advantage of the fact that most species of Collembola will float if submerged in liquid. Soil is flooded, stirred vigorously and allowed to stand for a few minutes. The springtails can then be picked off the surface film, or filtered from the liquid using a sieve with a fine mesh (Grossman 1988; Hale 1964a). The flotation technique is used to extract *Folsomia candida* from artificial soil in the standard ecotoxicological test (see Fig. 10.2).

9.3 Distribution of Collembola in space and time

9.3.1 Dispersal

Because Collembola are so small, and are unable to fly, there is a tendency to regard them as rather sedentary creatures that are unable to migrate over long distances. This is probably true of most euedaphic species which stay very much in one place unless they are forced to move through lack of food or pollution (Bengtsson *et al.* 1994a,b). However, in surface dwellers, this is far from the case (Grinbergs 1960; Lyford 1975). Even apparently slow-moving springtails such as *Hypogastrura socialis* can migrate more than 300 m in one day using the sun as a navigational aid (Hågvar 1995; Figs. 9.1, 9.2).

A very important mechanism of dispersal of Collembola, and other small invertebrates, is the wind. Freeman (1952) cited several examples of springtails being captured on sticky traps, or in nets towed from aeroplanes, at heights in excess of 3000 m. Species of '*Onychiurus*, *Entomobrya*, *Seira*, *Orchesella*, *Tomocerus*, *Bourletiella* and *Sminthurus*' were among those present in the samples. The same author also collected live Collembola in nets flown from wireless masts more than 80 m above the ground. On the Antarctic continent, Collembola have been caught in aerial traps at a latitude of 77°S (Gressitt *et al.* 1960).

In the past it has been assumed that such aerial dispersal was accidental. However, at certain times of the year, millions of individuals of a species of *Cryptopygus* in eucalyptus forest in New South Wales, Australia, undergo a synchronised ascent of the trees. Farrow and Greenslade (1992) monitored this behav-

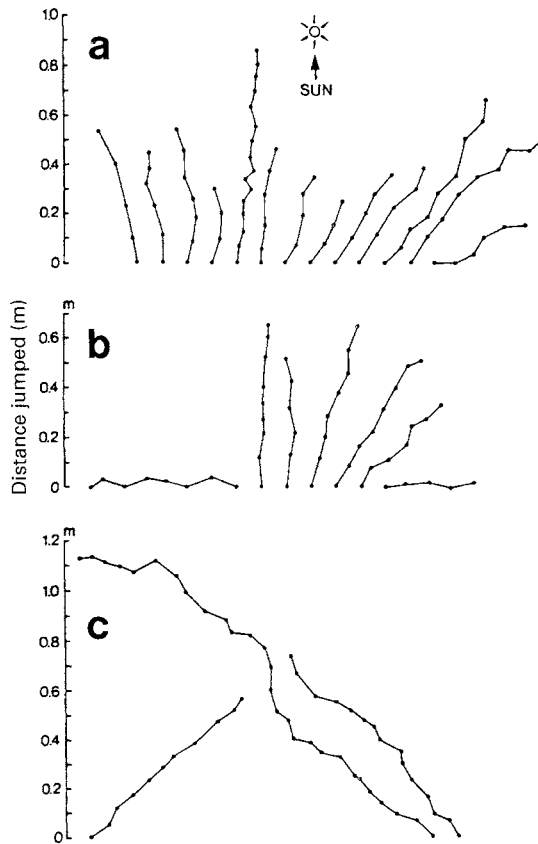


Fig. 9.1. Directional movements on Norwegian snow of individual *Hypogastrura socialis* (Hypogastruridae). Examples from three different populations (a,b,c). Dots indicate starting points for each jump. The animals moved towards the sun. Reproduced from Hågvar (1995) by kind permission of the author and the Finnish Zoological and Botanical Publishing Board.

ious on a single tree and counted some 10 000 individuals ascending per hour. They suggested that this behaviour increased the likelihood of the springtails being carried away by air currents which were stronger at the tops of the trees than near the ground. The ascent started at 11:00 on the morning of 4 April 1989, had finished by the late afternoon, and was not repeated that night or on subsequent days. Blackith and Disney (1988) provided a similar explanation for the climbing behaviour of *Salina celebensis* and an undescribed species of *Lepidocyrtus* in Toraut Forest, Sulawesi, Indonesia. Furthermore, they suggested that the exuviae of moulting specimens were retained by the animals to act as 'sails' to aid their dispersal by the wind.

One way of assessing the powers of dispersal of Collembola (and other animals) is to monitor the development of the fauna of new islands produced by volcanic activity. One such example was a small island which emerged from the sea in

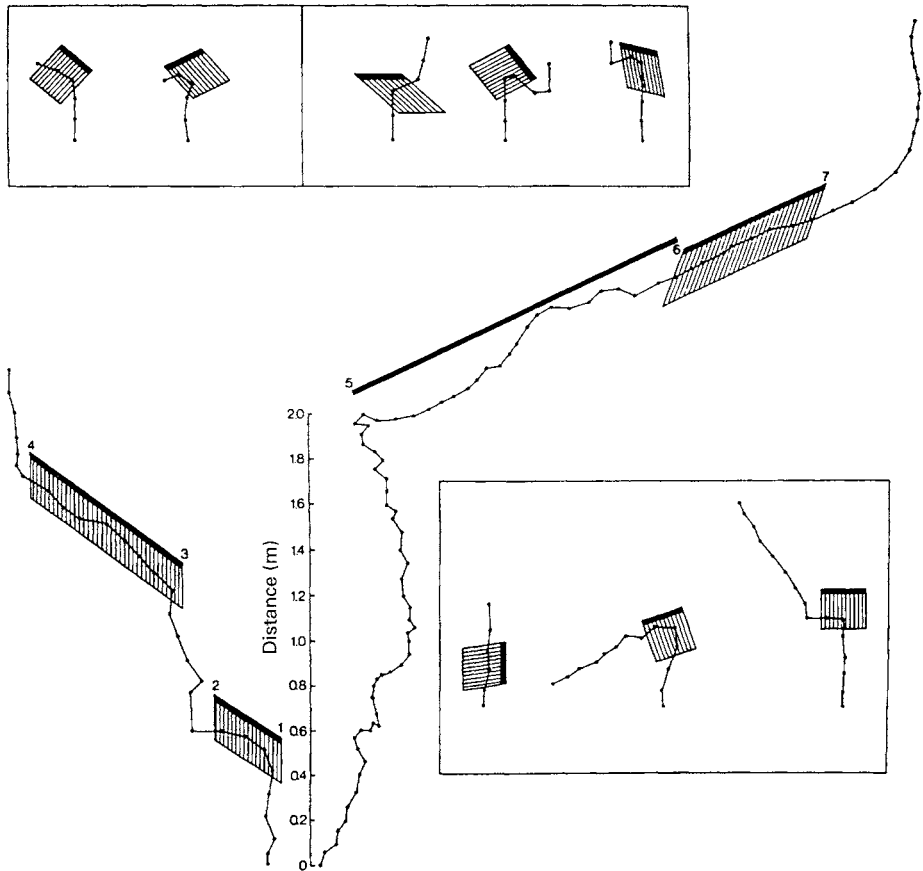


Fig. 9.2. Examples of the ability of individual *Hypogastrura socialis* (Hypogastruridae) to avoid dark obstacles on Norwegian snow. Dots indicate starting points for each jump. A thick line represents the obstacle and hatched area the shadow. Each animal moved towards the top of the figure. Reproduced from Hågvar (1995) by kind permission of the author and the Finnish Zoological and Botanical Publishing Board.

1929 about 4 km from Krakatau. When W.S. Bristowe visited the island in February 1931 he found numerous specimens of Collembola which were identified as *Mesira* (= *Lepidosira*) *calolepis*, a species also found on Java (Womersley 1932). Although there was no vegetation, a large amount of drift material had washed up on the beach and it was this which presumably carried the springtails onto the island. Oceanic drift is the most likely route that early collembolan colonisers of isolated islands such as Hawaii took to their new homeland (Christiansen and Bellinger 1992, 1994).

Human beings have transported many species of Collembola between biogeographical regions (Bellinger and Christiansen 1989; Greenslade 1987; Greenslade and Wise 1984; King *et al.* 1985). Greenslade (1987) estimated that of the 143

genera of springtails then known in Australia, 17 had been introduced. Most of these springtails probably travelled as eggs in soil surrounding the roots of plants, or in cultures of other animals. For example, *Onychiurus folsomi* was described as new to Spain by Arbea and Jordana (1988) who discovered this species as an abundant contaminant of soils in rearing beds for the earthworm *Eisenia andrei*. The isotomid collembolan *Proisotoma filifera* was discovered among a cucumber crop in glasshouses in Holland in 1968 where the springtails were so common that they formed grey patches on the soil (Ellis 1970). *P. filifera* is otherwise known only from Costa Rica and Peru (Mari Mutt and Bellinger 1990). The genus *Proisotoma* often occurs in such mass eruptions in synanthropic environments far from its original habitats (Ellis 1970). Such abundance is typical of introduced species which often expand rapidly in numbers due to the lack of natural predators and parasites. Many of these species have become established in the wild and have become more common than the native Collembola.

9.3.2 Aggregation

The density of springtails in soil and leaf litter is usually expressed as the number per square metre. However, this simple statistic does not take account of the fact that soil is a three-dimensional environment and that Collembola are not usually distributed evenly within it (Booth and Usher 1985; Joosse 1970; Milne 1962; Usher and Booth 1984, 1986). For example, Usher (1969) studied the lateral and vertical distributions of Collembola in blocks of soil and litter from a forest of Scots pine (*Pinus sylvestris*) in Scotland. He found that there were three main distribution types in the 12 species he studied:

- uniform distribution in 0.9% of the blocks (shown only by adults of *Folsomia quadrioculata*)
- random distribution in 27.4% of the blocks
- aggregated distribution in 71.7% of the blocks.

The results for juvenile *Pseudisotoma sensibilis* (Fig. 9.3) show clear evidence of lateral and vertical aggregation.

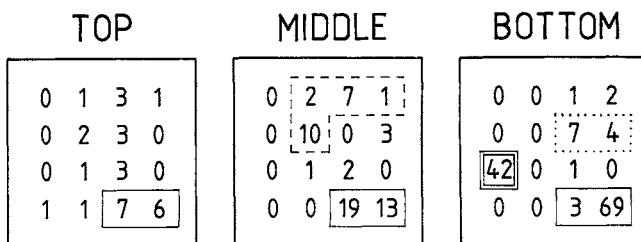


Fig. 9.3. Numbers of juvenile *Pseudisotoma sensibilis* (Isotomidae) in three layers of a block of soil taken from a Scottish pine forest. The animals were concentrated in four main aggregations each surrounded by dotted, solid, dashed or double lines. Redrawn from Usher (1969) by kind permission of the author and the British Ecological Society.

Field biologists are familiar with the tendency for many soil arthropods to form aggregations. These may form for two main reasons. First, animals may be attracted to ideal conditions of moisture (Joosse 1970, 1971; Joosse and Verhoef 1974; Nosek 1981; Vannier 1971; Verhoef and Nagelkerke 1977; Verhoef and Van Selm 1983), food (Barra and Christiansen 1975; Christiansen 1970c), or soil or leaf litter with pore spaces of a particular diameter (Kamplichler and Hauser 1993; Stevenson and Dindal 1982; Vannier 1975a). In 'difficult' environments, springtails are forced to aggregate in 'islands' where fluctuations in temperature and moisture are less extreme. For example, in trees, springtails frequently collect in moist nooks and crannies under bark or in epiphytes. In sand dunes or on lake margins, Collembola are often concentrated around compacted stems and roots of tussocks of grass (Hertzberg *et al.* 1994).

The second main reason for coming together of Collembola is the production of aggregation pheromones (Krool and Bauer 1987; Leonard and Bradbury 1984; Verhoef *et al.* 1977a,b). Pseudoscorpions are able to follow concentration gradients of these pheromones to guide them to their prey (Schlegel and Bauer 1994). The driving force for pheromone-led aggregation is probably the need for male and female Collembola to come together during sexual reproduction. There is an increased tendency for aggregations to form at high population densities (Usher and Hider 1975; Vegter *et al.* 1988b).

9.3.3 Vertical distribution

The ecological niches of some species of Collembola may appear to overlap considerably if they occupy the same habitat such as dead wood (Vannier and Kilbertus 1984), or if they feed on very similar diets (Vegter 1987). However, if one looks hard enough, there are invariably aspects of their life histories and behaviour which are clearly separate (Rusek 1979a). These include differences in vertical distribution of particular stages of the life cycle at different times of the year (Betsch and Vannier 1977; Bowden *et al.* 1976; Dunger and Schulz 1989; Hijii 1989; Itoh 1991; Lambert 1973).

The broad categories of euedaphic, hemiedaphic and epedaphic springtails are useful for giving a preliminary idea of the lifestyles of different species of Collembola (Lucianez and Simon 1989a). They are based primarily on the tendencies of different species to live out their lives in a particular vertical horizon between the tops of the trees and the deepest layers of soil. Most Onychiuridae spend all their lives in the soil and humus layers, and have lost pigment, eyes and the furca (Glasgow 1939; Takeda 1983). However, many other Collembola have broader vertical distributions (Hågvar 1983; see also Poole 1961 and the similar paper by Choudhuri 1962; Figs. 9.4–9.6). Although a species may be categorised as hemiedaphic, under certain circumstances, individuals may climb trees or crawl into soil. Earthworm burrows, for example, provide easy routes into deep soil for species that would otherwise find it difficult to squeeze between soil particles (Marinissen and Bok 1988).

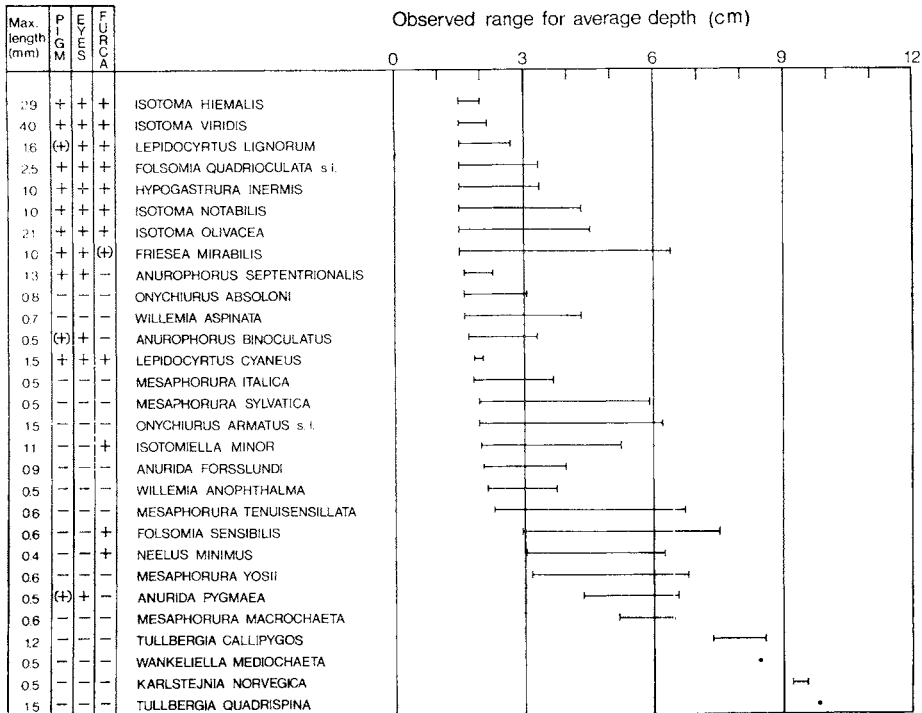


Fig. 9.4. Ranges of depths of the most common species of Collembola found in Norwegian coniferous soils. Note the tendency of euedaphic species to lose pigment, eyes and furca. Reproduced from Hågvær (1983) by kind permission of the author and Gustav Fischer.

9.3.4 Temporal variations in distribution in three dimensions

We have seen in the above examples that springtails are not distributed evenly throughout their environment. In addition, most species undergo various degrees of lateral or vertical movement which can be quantified by taking regular 'snapshots' of their distribution and activity (Filser and Fromm 1995; Greenslade and Greenslade 1973; Joosse 1965; Massoud *et al.* 1983; Poole 1962). The main driving force for migration is the search for ideal microclimates (Hijii 1987; Mateos 1991; Sgardelis *et al.* 1993; Usher 1970). Thus in very dry periods, species which one would normally find in superficial habitats such as *Allacma fusca* and *Orchesella flavesceus* (Bauer 1979) may crawl down into deeper layers of leaf litter and soil where they survive until it rains again (Kamplichler 1990).

Springtails which live in deserts show diurnal movement between the surface in the cool of the night and leaf litter during the heat of the day (Mackay *et al.* 1987). The same behaviour is observed in species of *Entomobrya* which venture onto roofs at night when the tiles have cooled down (Moon and Gough 1972). In Greenland, *Isotoma violacea* exhibits the opposite of this behaviour by being most active during the relative warmth of the middle of the day, and migrating down to

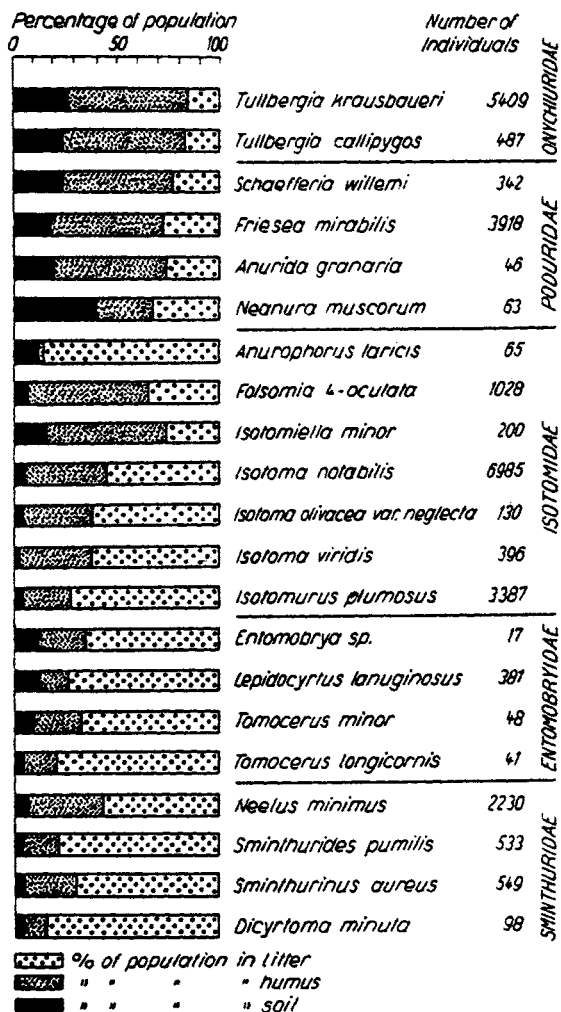


Fig. 9.5. Distribution of Collembola found in a Welsh coniferous forest soil. Reproduced from Poole (1961) by kind permission of the author and Gustav Fischer.

the deeper layers of leaf litter during the night when air temperatures drop to below -3°C (Fox and Stroud 1986). As one might expect, the distribution and behaviour of littoral species is synchronised with the tidal cycle (Debruyne 1988).

However, there are other explanations for short-term migrations. These include reproductive cycles (Curry 1971), the presence of preferred food types (Faber and Joosse 1993; Gerdsmeyer and Greven 1991a; Poole 1964), soil chemistry (Mateos 1988), the type of crop in agricultural soils (Snider *et al.* 1990) and type and state of decay of leaf litter (Teuben and Smidt 1992). In some cases, there may be no clear cause at all (Nijima 1971).

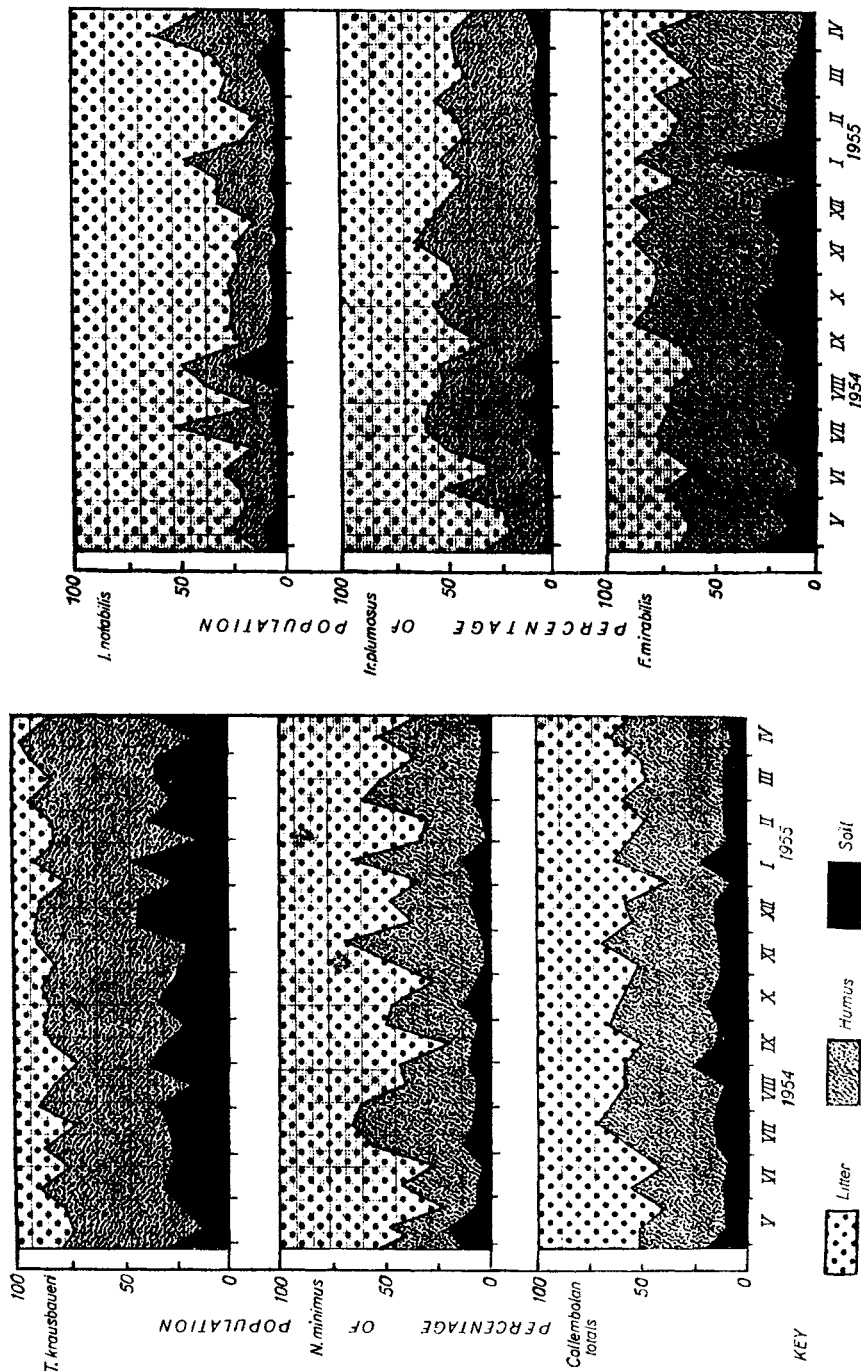


Fig. 9.6. Variations in the vertical distribution of the five most common species, and total numbers of Collembola found in a Welsh coniferous forest soil. (cf. Fig. 9.5) Reproduced from Poole (1961) by kind permission of the author and Gustav Fischer.

Movement of individual species towards particular areas may be difficult to assign to a single factor. The cause of the attraction may also change with time (Klironomos and Kendrick 1995a). Since wet areas are where fungus grows best, it is difficult to decide whether aggregations of Collembola that form in such sites have gathered in response to moisture or a preferred food supply. Hassall *et al.* (1986a) managed to separate these factors by showing that the driving force for upward migration of *Onychiurus subtenuis* in Canadian soils is the presence of specific microorganisms which 'bloom' after a rainstorm (Fig. 9.7). A similar conclusion was reached regarding species of *Tomocerus* in North American forests by Knight (1963) and Knight and Read (1969).

In addition to these short-term changes, springtails may also show long-term seasonal changes in distribution which are related to primarily to climate (Badejo and Van Straalen 1993; Gunadi 1994; Reddy and Toky 1990; Reddy and Venkataiah 1990a,c; Sinha *et al.* 1988). They move deeper in the soil profile to avoid frost or dryness and emerge when it warms up or rains. In India for example, many species of Collembola show highly synchronised behaviour by all coming to the surface when the monsoon breaks (Mukherjee and Banerjee 1993; Reddy 1992). However, in Japanese forests *Tomocerus cuspidatus* and *Sminthurus arborealis* take advantage of reduced competition by remaining active in trees during the winter (Hisamatsu and Matsunaga 1994; Itoh 1994a). Some hypogasturids exploit the 'vacant' winter niche by remaining active on the surface of snow (Leinaas 1981a,b,c).

Seasonal migrations may also be connected with reproductive activity. Adults of *Entomobrya nivalis* live in trees for most of the time. However, the females descend to the ground to lay their eggs in the litter layer where the first two juvenile instars live before climbing up into the branches to join their parents (Turner 1983; Von Allmen and Zettel 1982).

9.3.5 Succession

The climax community of plants which develops at a particular location on the Earth is related mainly to climate. Thus in moist tropical areas, the climax community is rainforest whereas in polar regions where trees cannot survive, the vegetation consists of mosses and lichens which grow little more than a few centimetres above the soil surface. Geology is also important and the species of plant which develop on a calcareous soil derived from limestone bedrock will be very different from the vegetation of a sandy area where conditions are acidic. These and other factors (Section 9.4) influence which species of Collembola are present in a particular habitat at a specific time.

When a stable climax community of vegetation has been established, the number of species of springtails stays fairly constant over time if the habitat remains undisturbed. The collembolan fauna typically comprises a few common species, and a larger number of rarer species with much lower dominance values (Bödvarsson 1961, 1967; Curry 1969; Gerdsmeyer and Greven 1991a; Kamplichler 1992; Kopeszki and Meyer 1994; Röske 1989; Fig. 9.8). The total

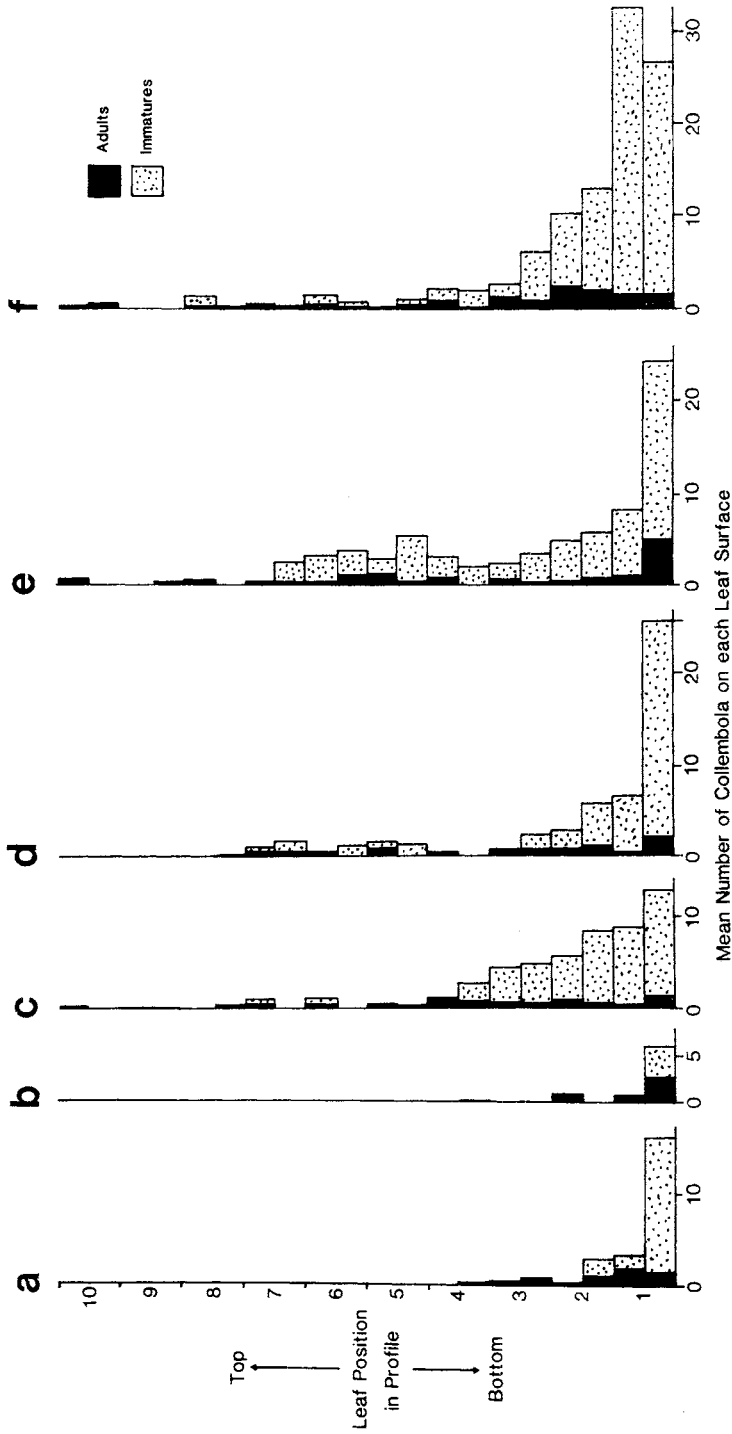


Fig. 9.7. Distribution of *Onychiurus subtenis* in microcosm litter profiles 13 h after introduction of leaf lamina that had been autoclaved and reinoculated with various microorganisms. (a) control, (b) basidiomycete 290, (c) bacteria, (d) *Mortierella*, (e) *Cladosporium*, (f) yeast. Reproduced from Hassall *et al.* (1986a) by kind permission of the authors and Gustav Fischer.

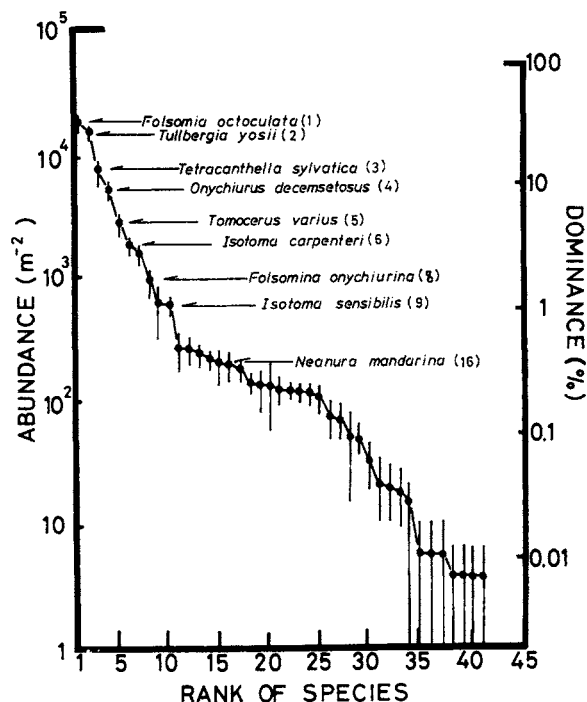


Fig. 9.8. Relative abundances of collembolan species as percentages of the sum of the overall mean abundance for all collembolan species, and mean abundance m^{-2} over a 15 year period in a Japanese red pine forest. Bars indicate standard errors. The species are categorised as dominant ($>1\%$), rare ($0.1\text{--}1\%$) and very rare ($<0.1\%$). Reproduced from Takeda (1987) by kind permission of the author and the Japanese Society of Population Ecology.

numbers of individual Collembola and relative abundances of species may fluctuate with time (Figs. 9.9, 9.10) but there are few extinctions or immigrants (Takeda 1987). Different climax communities may have characteristic assemblages of species (Section 9.4).

In heavily disturbed habitats, or ecosystems which are developing through succession, the assemblage of species of Collembola may be different from that of the eventual climax community. In general, the number of species increases with time, but some species drop out and others appear during the succession (Bolger 1985; Petersen 1995; Usher 1985; Usher *et al.* 1982). 'New' environments are rapidly colonised by so-called 'pioneer' species such as *Bourletiella hortensis* (Tamm 1986b) which may be replaced by others as the succession progresses (Hutson 1980a,b; Palacios-Vargas and Castillo 1992).

Some of the clearest examples of succession occur following deliberate or accidental burning (Betsch and Cancela da Fonseca 1995; Broza *et al.* 1993; Greenslade 1993; Mateos and Selga 1991; Metz and Farrier 1973; Oliveira and Franklin 1993; Prabhoo and Pai 1986; Reddy 1983; Takeda 1981). However, the effects of fire may not be as drastic as one might expect. In a burning deciduous

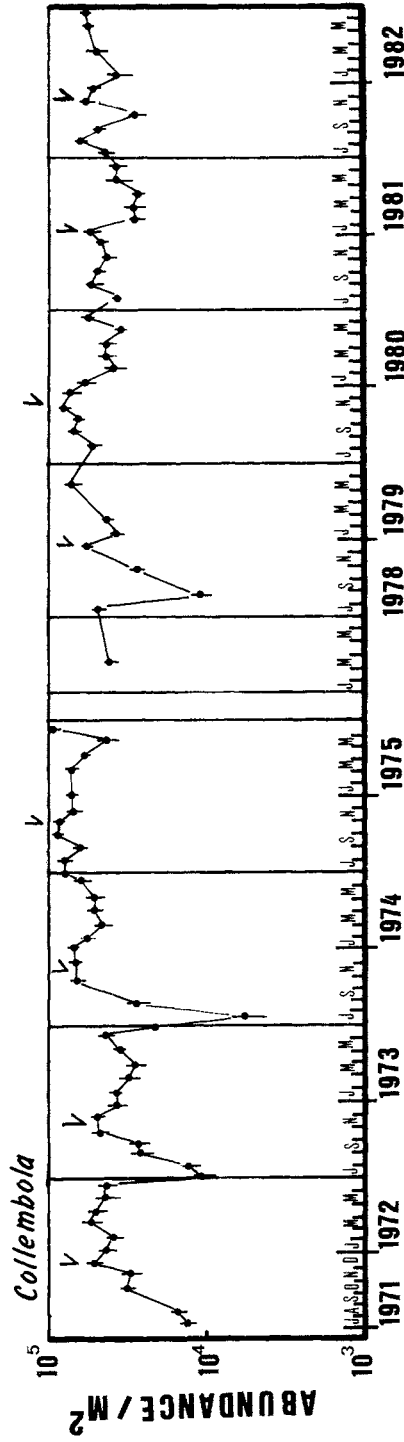


Fig. 9.9. Changes in total abundance of Collembola with time in a Japanese red pine forest. Bars indicate standard errors. Arrows indicate the winter population break. Reproduced from Takeda (1987) by kind permission of the author and the Japanese Society of Population Ecology.

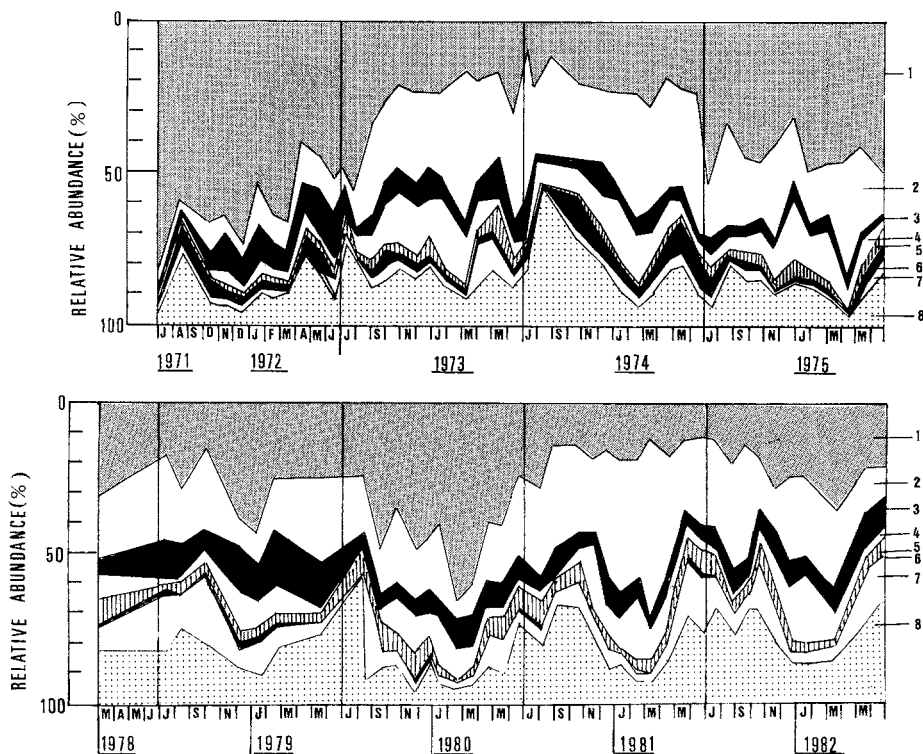


Fig. 9.10. Changes in relative abundances of Collembola with time in a Japanese red pine forest (1) *Folsomia octoculata*, (2) *Tullbergia yosii*, (3) *Onychiurus decemsetosus*, (4) *Tetracanthella sylvatica*, (5) *Isotoma carpenteri*, (6) *Isotoma sensibilis*, (7) *Tomocerus varius*, (8) other species. Reproduced from Takeda (1987) by kind permission of the author and the Japanese Society of Population Ecology.

oak forest in France, Vannier (1978*b*) measured a temperature of 480°C in the leaf litter, but at a depth of 2.5 cm, the temperature did not exceed 20°C. Thus species at or below this depth survived the fire. Many persisted as eggs which, when they hatched, were able to take advantage of the lack of competition before the habitat was recolonised from unburnt areas. Waste tips derived from mining activity also provide interesting demonstrations of the importance of Collembola in early succession when earthworms are absent (Davis 1963; Dunger 1978*b*; Greenslade and Majer 1980, 1993; Hutson 1980*a,b*, 1981; Moore and Luxton 1988; Parsons and Parkinson 1986).

Ideally, succession should be followed by regular sampling of a habitat over time. This is possible for communities which develop relatively rapidly. For example, there is a succession of Collembola on dead wood which correlates with successive 'waves' of fungal species adapted to exploit different components of the wood (Seastedt *et al.* 1989). Similar 'real time' studies can be performed by monitoring the species present during the decomposition of leaf litter (Hågvar and Kjondal 1981*a*; Lagerlöf and Andrén 1985; Siepel 1990; Siepel and Van Wieren

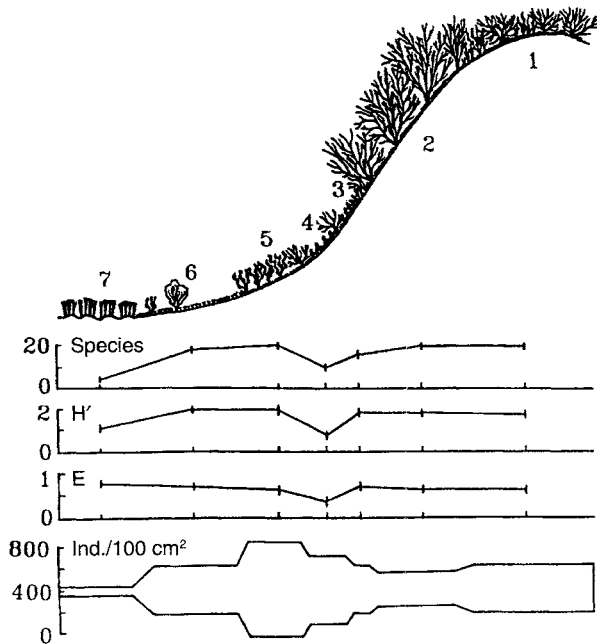


Fig. 9.11. Transect through the edge of a pingo lake in Canada showing number of species, Shannon-Wiener index of diversity (H'), evenness (E), and density of Collembola. Reproduced from Rusek (1994) by kind permission of the author and the Finnish Zoological and Botanical Publishing Board.

1990; Uvarov 1994). Springtails are very important in 'kick-starting' decomposition processes soon after leaf litter falls to the ground by direct feeding, consumption of fungal hyphae and transport of fungal spores to deeper layers (Takeda 1995). However, on the broader scale, direct observation of complete succession from bare soil is not practical for communities such as temperate deciduous woodland which may take more than 100 years to achieve stability. In very cold climates, climax communities may take 200 years or more to become stable (Hågvar *et al.* 1978).

An alternative approach, is to examine ecosystems at different stages of development under the assumption that they will all follow a similar path to the same climax community (Parr 1978; Setälä and Marshall 1993, 1994; Setälä *et al.* 1995). On the margins of lakes where there is a gradient of habitat types, the abundance and diversity of species changes as the succession advances (Rusek 1994; Fig. 9.11).

9.4 Collembola as ecological indicators

9.4.1 Introduction

In recent years, there has been widespread interest in using animals as 'ecological indicators' of the state of the environment (the use of Collembola as biological

monitors of pollution is covered in Chapter 10). Characteristic communities of species may highlight properties of natural habitats that would be difficult or impossible to quantify by simply measuring physical factors or vegetation type (for a recent review see Van Straalen, in press). One of the clearest examples of the use of such 'community fingerprints' in insects is for paleoclimatic reconstruction. Beetles are identified in Quaternary sediments in which they may remain in a good state of preservation for many thousands of years. If these species are extant, and their temperature preferences are known, then their presence in a particular deposit can be used to indicate the temperature of the environment in which the beetles were preserved (Coope 1995).

In Collembola, three main approaches have been adopted to elucidate why species are present within specific habitats. In the first approach, attempts have been made to correlate presence with abiotic and biotic factors (Section 9.4.2). In the second, presence is correlated with microhabitat type in a large number of similar ecosystems (Section 9.4.3). Third, lists of species are drawn up to highlight characteristic assemblages in different habitats (Section 9.4.4). This information is drawn together in the study of species successions, and the effects of changes of land use and agricultural practices on collembolan communities (Section 9.4.5).

Ecological monitoring contributes to informed conservation. One of the aims of such work is to enable us to predict succession of the fauna and flora of a habitat if we burn it, clear fell and plant non-native trees, spray it with insecticide, or alter it in some other way. However, before such predictions can be made, detailed knowledge is required of the communities of species of these ecosystems, how they may change over time and the factors which affect their make up (Bengtsson 1994).

9.4.2 *Correlations between presence or absence of Collembola and other factors*

The main thrust of this approach is to define which climatic or biological features of habitats are most important in dictating the distribution of Collembola. If the factors can be identified then in theory one could predict which species will be present simply from a description of these characteristics. The approach is potentially useful for predicting the effects on springtail communities of land-use change or succession of vegetation.

The wider distributions of some species of springtail can be related to simple climatic factors. For example, the northern limit of *Sminthurus viridis* in Norway and Finland is defined by a line joining localities that experience a mean temperature of 10°C on at least 100 consecutive days in the year (Wallace 1973). However, except in extreme environments such as deserts or polar regions, the heterogeneity of natural ecosystems is so great that it is difficult to make similar predictions on a local scale from climatic data alone. The only way in which such a large number of factors can be considered simultaneously is by using multivariate statistical techniques (Arbea 1989; Arbea and Jordana 1987, 1990a; Bolger

1984; Bonnet *et al.* 1975, 1977, 1979; Gama *et al.* 1989b; Lucianez and Simon 1988, 1989a,b, 1992a; Parr 1978; Poursin and Ponge 1984; Pozo 1986; Pozo *et al.* 1986; Rusek 1992; Setälä *et al.* 1995). Unfortunately, such studies rarely identify a single factor as the dominant influence on distribution. Among the parameters which may contribute are temperature, soil type, soil moisture content, soil pH, presence or absence of a leaf litter layer and characteristics of the fungal community (Betsch 1991; Betsch and Cancela da Fonseca 1995; Hashimoto and Tamura 1994; Klironomos and Kendrick 1995a; Kovác 1994; Ponge *et al.* 1993).

In habitats such as tropical forests, it may be difficult to correlate species richness or composition on a local scale with any abiotic factors (Deharveng and Bedos 1993a). Microclimates are so diverse that it is impossible to measure cycles of temperature and humidity in them all. The habitat feature that might seem to have the most influence on Collembola is vegetation type. However, there are few examples of direct correlations between specific Collembola and particular species of plants. It is difficult to separate direct effects from indirect effects such as level of shade, moderation of climatic extremes and physical structure of the branches and leaves (Ellis 1974b). Some authors such as Al-Assiuty *et al.* (1993) and Natuhara *et al.* (1994) have found no correlation with vegetation type at all. However, there may be an indirect relationship with the type of humus formed from the decaying leaves (Ponge 1993). From his studies on Norwegian forests, Hågvar (1982) concluded that the more extreme the climatic conditions, the better the correlation between vegetation type and the collembolan fauna.

The multivariate approach is useful in identifying trends but the data is too equivocal to be of widespread practical use without a massive increase in the number of sites studied. One of the problems is that a correlation with a specific factor such as soil chemistry obtained at one time of the year may not persist at other times (Hågvar and Abrahamsen 1984). That is not to say that characteristic species are never found in particular habitat types (Agrell 1963; Christian and Kampichler 1984), but that it is difficult to pin down the exact reasons for their presence or absence to a sufficient degree of accuracy for widespread use of the technique.

9.4.3 *Habitat preferences*

In view of the difficulty of identifying the factors that limit the local distribution of Collembola, is it possible to take a broader view and look for consistent microhabitat preferences? J.F. Ponge has performed some of the most comprehensive studies of this type within Atlantic temperate forests of Northern France (Ponge 1983, 1993; Ponge and Prat 1982). Samples of Collembola were taken from 679 forest sites and the associations of each species with 56 microsites were recorded. He found 145 species in total and included just over 100 of these in the statistical calculations (44 species were found in less than five samples and were not included in the analysis). When the data was subjected to correspondence analysis (one of the projections is shown in Fig. 9.12), certain species showed clear associations with particular environments. Some of the conclusions were not surprising

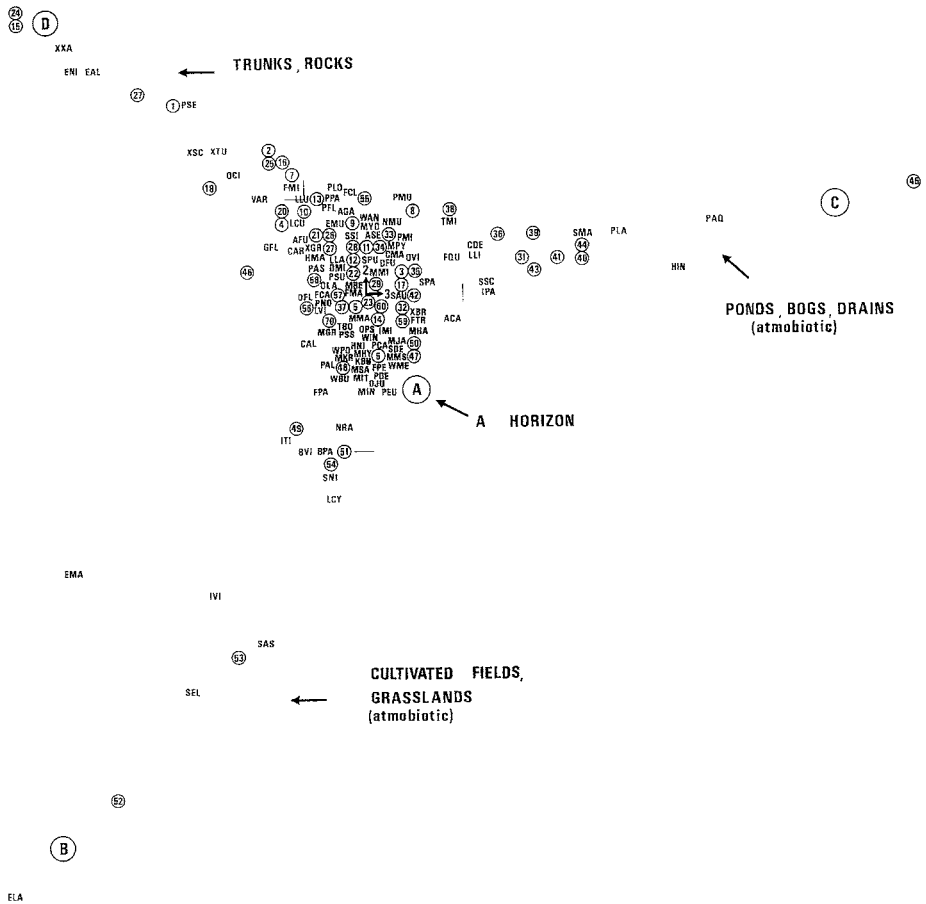


Fig. 9.12. Correspondence analysis projected in the plane of the axes 2 and 3 of the microhabitat preferences of 100 species of Collembola collected from 679 Atlantic temperate forest sites in Northern France. Some species show clear preferences for certain habitats e.g. *Entomobrya albocincta* (EAL), *Entomobrya nivalis* (ENI) and *Xenylla xavieri* (XXA) for tree trunks and rocks, *Entomobrya lanuginosa* (ELA) for cultivated fields and grasslands, and *Heterosminthurus insignis* (HIN) and *Podura aquatica* (PAQ) for ponds, bogs and drains. The numbers refer to microhabitat types, e.g. 45 = water surface. Reproduced from Ponge (1993) by kind permission of the author and Gustav Fischer.

(*Podura aquatica* associated with ponds, bogs and drains, *Entomobrya nivalis* showing a preference for tree trunks and rocks etc.) but overall, Ponge's work is important because it provides a very comprehensive data set which can be compared statistically with other similar surveys in the future.

9.4.4 Lists of species

One of the problems with multivariate analysis is the difficulty of incorporating rare species; they occur in too few sites for meaningful correlations to be obtained.

However, habitats which enjoy the greatest legal protection are those which contain the rarest species. Rare species often have the most specialised habitat requirements (otherwise they would be common) and are potentially of great use in indicating that a particular habitat is 'special', even unique. Therefore, the preparation of lists of species from as wide a range of sites as possible is likely to be the main method for the foreseeable future of assessing conservation priorities for under-recorded groups such as Collembola. The fact that ecological surveys in countries such as Australia still turn up numerous undescribed species illustrates how much fieldwork still has to be done (Greenslade and Thompson 1981).

9.4.5 Effects on Collembola of agricultural practices and changes in land use

Many parts of the Earth have been changed from their natural state through human activities. The effects on the soil fauna have been considerable (Rusek 1987a). Much effort has been expended in describing the effects of such changes on Collembola, and in predicting the likely effects of proposed habitat alterations.

There are two main approaches to this topic. First, the species of springtails in the altered habitat can be compared with one or more unaffected 'control' sites which it is assumed was the state of the new habitat before it was changed. For example, forest cleared for agriculture can be compared with adjacent uncleared areas (Miranda-Rangel and Palacios-Vargas 1992), and with plots which have been allowed to revert to secondary forest (Villalobos 1989). Second, the Collembola fauna in a site can be monitored before and after the alteration (burning, application of fertilisers, crop planting, etc.) if one has sufficient notice that a change is proposed or if it is part of a scientific monitoring experiment. Long-term succession of species can be followed for as long as resources are available (Rusek 1990).

The most widely studied factor is the impact of different agricultural and forestry regimes (the effects of pesticides are covered in Chapter 10). Practices which affect the abundance and species composition of Collembola include ploughing methods (Bertolani *et al.* 1989; Loring *et al.* 1981; Rickerl 1986; Rickerl *et al.* 1989), grazing pressures from sheep, cattle and rabbits (Argyropoulou *et al.* 1994; Bardgett *et al.* 1993a; Deharveng and Travé 1981; Desender *et al.* 1984; Greenslade and Greenslade 1987; King and Hutchinson 1980; King *et al.* 1976, 1985; Leetham and Milchunas 1985), crop type, rotation and harvesting conditions (Akkerhuis *et al.* 1988; Lagerlöf and Andrén 1991; Prabhoo 1986; Reddy and Venkataiah 1986), and forestation (Arbea and Jordana 1985a; Blackith 1974; Gama *et al.* 1991, 1994; Huhta and Mikkonen 1982; Jordana *et al.* 1987; Reddy and Venkataiah 1990a,b,c). Multivariate techniques have been used in attempts to highlight the factors which most influence Collembola (Dekkers *et al.* 1994) but these are very difficult to separate from other environmental influences (Filser 1995b).

The majority of these studies have shown that Collembola tend to increase their abundance during the early stages of change to agricultural use, especially if

fertilisers are applied at low to moderate levels (Bolger and Curry 1980; King and Hutchinson 1980; Kopeszki 1993a, 1994; Lübben 1989; Vilkamaa and Huhta 1986; Zettel and Klinger 1983). However, species diversity is reduced in comparison to the natural habitat and may take many years to recover if the site is left undisturbed (Rusek 1991f).

Other human activities that tend to decrease the abundance and diversity of euedaphic springtails include soil compaction through trampling (Massoud *et al.* 1984), vehicular activity (Aritajat *et al.* 1977; Heisler 1991, 1994; Heisler and Kaiser 1995), skiing (Bonnet *et al.* 1976) the spreading of artificial snow (Trockner and Kopeszki 1994) and general urbanisation (Pouyat *et al.* 1994; Sterzynska 1989). In sugar beet crops, compaction may be advantageous to the farmer in one sense as it inhibits the migration of the 'pest' species *Protaphorura fimata* (Didden 1987). However, hemiedaphic and epedaphic species such as *Isotoma notabilis* and *I. violacea* are less affected by the reduction in soil pore space and may increase in numbers (Kopeszki and Trockner 1994).

If a change of land use or agricultural procedure is planned, then the results of the studies cited above can be used to broadly predict the effects on the Collembola community. A successful model has been developed for predicting the effects of different agricultural practices on *Isotoma notabilis* (Diekkrüger and Röske 1995; Fig. 9.13), but it likely to be many years before this approach can be extended to all species.

9.5 Conservation

The principal aim of biological conservation on a global scale is to retain and increase biodiversity (Angermeier 1994; Harper and Hawksworth 1994; May 1994). However, before choices can be made as to which habitats should receive protection and sympathetic management (the 'agony of choice', Vane-Wright *et al.* 1991), information is needed on rarity of the species within them. The status of most terrestrial vertebrates is fairly well-known and informed decisions are possible. However, the global distribution of most invertebrates is poorly understood (Hammond 1994) and for individual species of Collembola, detailed knowledge is almost non-existent. The need to obtain this information is the strongest argument for comprehensive mapping of their distribution.

The United Kingdom has mapping schemes in progress for several invertebrate groups (but not yet Collembola). These are coordinated by the Biological Records Centre at Monks Wood near Huntingdon. Periodically, the records collected by contributors to each scheme are processed into distribution maps (one for each species) on which the presence or absence of a species is marked in each 10 km square of the Ordnance Survey Grid. When a reasonable coverage of the country has been achieved, a level of rarity can be assigned and if necessary, the species can be entered into the British Red Data Book (RDB) and conservation measures taken. Thus, for a species to be considered 'rare' (RDB category 3), it must be present in fewer than 15 areas of 10 km². Although similar comprehensive schemes may eventually develop in other industrialised countries, the resources to

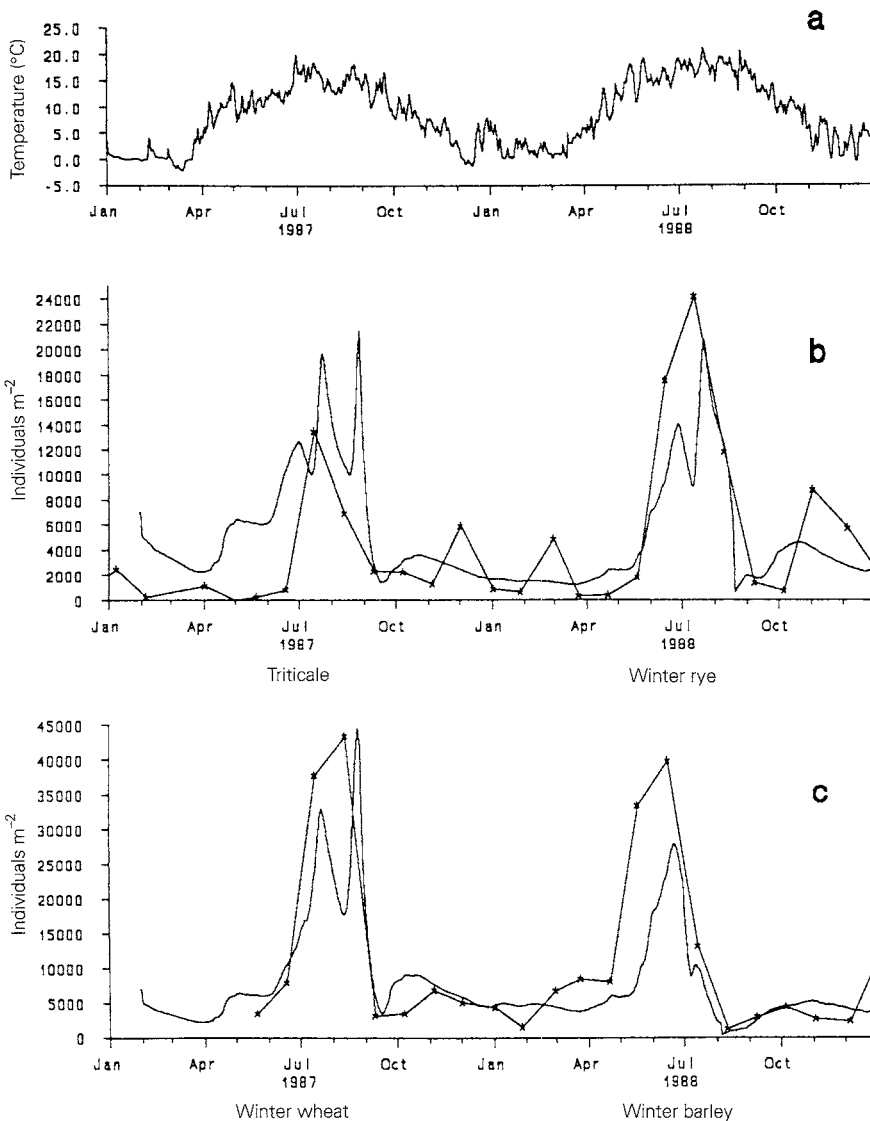


Fig. 9.13. Comparison between measured (*) and simulated population size of *Isotoma notabilis* (Isotomidae) on (b) peaty agricultural soil and (c) sandy agricultural soil in Germany. (a) Time course of soil temperature at a depth of 5 cm. Reproduced from Dieckkruger and Röske (1995) by kind permission of the authors and Gustav Fischer.

conduct these surveys are unlikely to materialise in tropical countries where the majority of species occur (Wilson 1992). At least the advent of the Internet has made it much easier to disseminate information on the biodiversity and global distribution of Collembola, and other animals (Allkin and Winfield 1993).

An alternative approach to conservation is to hope that nature reserves created to protect scarce 'high profile' plants and animals will also conserve the rarest species of Collembola and other soil invertebrates. However, this correlation does not always hold true (Prendergast *et al.* 1993). Countries such as Australia and New Zealand have numerous endemic species which may be quite local in their distributions. Clearing of native habitat and conversion to grazing land is considered a major threat in New South Wales, Australia where endemic Collembola may become extinct unless the habitats they occupy can be identified and conserved (Greenslade and Crawford 1994).

The most recent estimate of the number of species on Earth is 13–14 million, only 13% of which have been described (Heywood 1995). If this same ratio of described (around 6500, see Appendix A) to undescribed species is applied to Collembola then at least 45 000 species are waiting to be discovered. The majority of these are likely to be in the soil, leaf litter and trees of tropical rain forests (André *et al.* 1994; Deharveng *et al.* 1989; Stork and Eggleton 1992). However, Platnick (1991) has made a plea for temperate habitats not to be ignored as they may contain pockets of relict species which are globally rare.

It is inevitable that many undescribed species will become extinct before any human has seen them, let alone given them a name. Once biodiversity is lost through extinctions, it takes many millions of years to recover (Signor 1994; World Conservation Monitoring Service 1992).

9.6 Cave Collembola

The biology and distribution of cavernicolous Collembola have been extensively reviewed in the recently published *Encyclopaedia Biospeologica* edited by Juberthie and Decu (1994). This fascinating book contains an excellent article on Collembola by Thibaud and Deharveng (1994), together with extensive biogeographical information on cave springtails, so the subject will be covered relatively briefly here. Also well worth reading is the thought-provoking paper by Christiansen (1992*b*) in which the value of biospeological research in relation to general evolutionary theory is discussed.

The presence of Collembola in caves has been known for many years (e.g. Carpenter 1897; Wright and Haliday 1857). Most caves occur in limestone areas but Collembola have also been found in lava tubes in Hawaii (Bellinger and Christiansen 1974), lava caves in South Korea (Thibaud 1993*b*) and wind tubes in the Lower Austrian Prealps (Christian 1993*a*). Checklists of cave Collembola from particular countries are cited in Appendix B. Caves in limestone areas are vulnerable to complete destruction through quarrying, but the main threat to very deep caves comes from pollution of ground water.

Caves are very interesting from a biogeographical point of view as they provided refugia during glaciations and are home to 'relict' species (Deharveng and Thibaud 1989*b*). Many are closed systems isolated from the surface and have been stable for many millions of years. In most caves, humidity is close to 100% and temperatures vary little from 10°C (Thibaud 1970). Thus surface species which make their way into these caves enter a frost-free environment with little or no cli-

matic variation. They may undergo adaptive radiation and become endemic to that cave system (Christiansen and Culver 1969). Parallel speciation may occur where morphologically similar species arise independently in different caves in response to common selective pressures (Christiansen 1961, 1965). Thus the characteristics of *Pseudosinella hirsuta* appear to have evolved independently in at least four different caves in North America (Christiansen and Culver 1968).

Recent work divides cave Collembola into three main categories (for reviews see Thibaud 1986, 1991*b*, 1994*a*):

- *troglobites* are only found in caves
- *troglophiles* live in caves, soil and related environments
- *trogloxenes* are occasionally found in caves but their presence is temporary.

Troglobites are fairly easy to recognise as they exhibit reductions in certain physical characteristics, but the latter two forms may be difficult to distinguish from non-cavernicolous springtails. About 15% of the species of Collembola found in caves are troglobites (Massoud and Thibaud 1977).

The 'regression' of physical characters in troglobites has been recognised for more than 100 years (e.g. Packard 1888). These include the partial or complete loss of eyes (Barra 1973; Christian 1983; Christian and Schaller 1982; Thibaud 1976*a*; Thibaud and Massoud 1973*b*; Thibaud-Brauner 1985), reduction or loss of pigment and furca, and elongation of the claw and empodial appendage (Fig. 9.14). Reductions in eyes, furca and pigment are also seen in some euedaphic Collembola. However, lengthening of the claw and empodium is only found in cave animals and is associated with movement over wet surfaces and water (Christiansen 1965, 1985; Deharveng and Gouze 1986).

Cave-adapted species show several differences in reproduction, physiology and behaviour in comparison to non-cave-adapted Collembola (Barra 1991; Thibaud and Vannier 1986). These features include greater intrapopulation variability (Christiansen and Bouillion 1978*b*), lower fecundity and slower embryonic and post embryonic development (Lee and Kim 1995*a*; Lee and Thibaud 1987; Thibaud 1968*a,b*, 1969, 1970), increased levels of fat but decreased water content and ability to regulate water loss, and reduced respiratory metabolism (Thibaud 1980*a*; Thibaud and Vannier 1978, 1980; Vannier 1977*a,b*; Vannier and Thibaud 1978, 1984). There is also greater resistance to fasting accompanied by a tendency to ingest soil particles from which microflora may be removed in the digestive system (Kilbertus and Vannier 1981; Thibaud 1981). The main sources of food are detritus washed into caves from the surface, fungus, and bat guano which provides a rich source of minerals (Palacios-Vargas and Gnasparini-Netto 1992; Thibaud and Vannier 1969; Vannier and Thibaud 1971).

Representatives of most families of Collembola can be found in caves. These include Hypogastruridae (Lee and Kim 1995*a*; Lee and Thibaud 1987; Palacios-Vargas and Gnasparini-Netto 1992; Thibaud 1967, 1968*a,b*, 1969; Thibaud and Vannier 1969), Neanuridae (Deharveng 1987*e*), Onychiuridae (Deharveng 1979*a*; Deharveng and Gouze 1984), Entomobryidae (Deharveng and Thibaud 1989*b*),

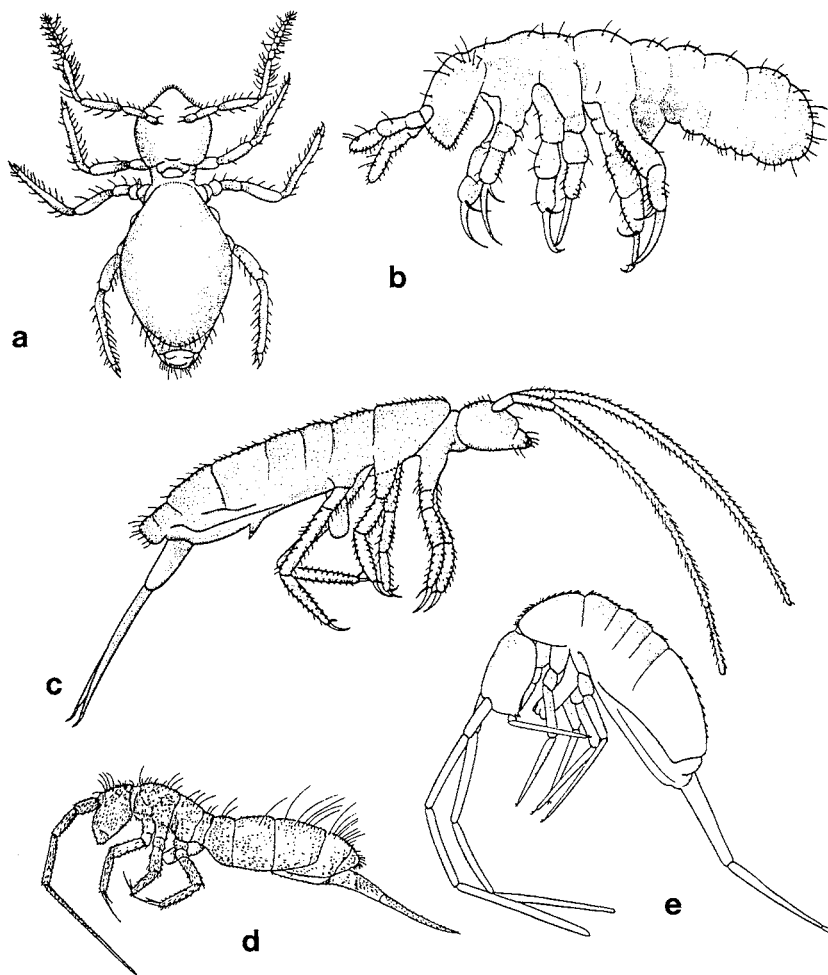


Fig. 9.14. Examples of 'cave Collembola': (a) *Arrhopalites pygmaeus* (Katianninae : Sminthuridae) from Europe; (b) *Ongulonychiurus colpus* (Onychiurinae : Onychiuridae) from Spain; (c) *Tritomurus falcifer* (Tomoceridae) from France; (d) *Bessoniella procera* (Orchesellinae : Entomobryidae) from France; (e) *Troglopedetes delamarei* (Paronellidae) from Cuba. Reproduced from Thibaud and Deharveng (1994) by kind permission of the authors and Laboratoire Souterrain du CNRS, Moulis, France.

Isotomidae (Deharveng 1989a), Oncopoduridae (Deharveng 1988d), Paronellidae (Deharveng 1988e; Palacios-Vargas and Wilson 1990; Wilson 1982), Tomoceridae (Vannier 1977a), Neelidae (Deharveng and Beruete 1993) and Sminthuridae, especially *Arrhopalites* (Nayrolles 1990c; Thibaud and Deharveng 1994). *Pseudosinella* (Entomobryidae) has undergone the greatest speciation of any genus with more than 100 species being found in caves (Christiansen and Moberg 1988; Christiansen *et al.* 1983, 1990; Deharveng 1988c; Deharveng and Gouze 1986; Stomp *et al.* 1991).

Ecotoxicology

10.1 Introduction

Ecotoxicology is concerned with defining the potential or adverse effects of chemical agents (derived either directly or indirectly from human activity in industry and agriculture) on natural ecosystems (for recent reviews see Calow 1989, 1993, 1994; Hopkin 1993*b*; Jørgensen *et al.* 1991; Kula 1992; Walker *et al.* 1996). In the context of this book, ecotoxicology is the study of the effects of such chemical agents on Collembola. A comprehensive list of references to laboratory and field studies of the effects of chemicals on Collembola is given in Appendix C.

Two main approaches have been adopted to study this problem. In the first approach, toxicity experiments are conducted with specific substances on one or other, of a relatively small number of species (Section 10.2). The information obtained may be used to predict the effects of the chemical in natural environments and to conduct risk assessment (Section 10.3). The second approach looks at affects of chemicals on natural populations of Collembola. A site is monitored before and after contamination, or impacted sites are compared with an unaffected, ecologically similar 'control' site nearby (Section 10.4). In recent years, microcosms have been developed where experiments are conducted in field enclosures, or intact soil cores are transported to the laboratory where conditions can be more tightly controlled.

Collembola are important prey items for many animals (Section 7.3.1) so the study of bioaccumulation of chemicals is important for predicting food chain transfer (Section 10.5). Populations of springtails in contaminated environments may evolve genetically distinct, resistant races which are more tolerant to pollutants than non-resistant populations (Section 10.6). The chapter ends with some general conclusions concerning the future role of ecotoxicology in studying the effects of chemicals on natural populations of Collembola (Section 10.7).

10.2 Laboratory toxicity tests with Collembola

10.2.1 Introduction

New drugs must be extensively tested over several years before they receive a license for use by humans. Pesticides are tested for vertebrate toxicity but until recently, there was little legal requirement to assess ecotoxicity, in other words the effects of the chemical on natural environments. However, increased environmental awareness has led to the introduction of tests for non-target organisms. For soil



Fig. 10.1. Adults and juveniles of parthenogenetic *Folsomia candida* (Isotomidae). The largest specimen is 2 mm in length. Photograph by Steve Hopkin.

animals, the standard test using the earthworm *Eisenia fetida* is now widely used (see Van Gestel and Van Staalen 1994). The next test which is likely to become routine uses the isotomid collembolan *Folsomia candida* (Fig. 10.1) which has been the subject of numerous toxicity tests (see Appendix C).

The main criticism of standard testing procedures is the artificial conditions under which the animals are kept. The temperature is uniform, humidity is constant, there are no predators and the standard soil bears little resemblance to natural field soils. Furthermore, the animals are restrained within the test containers. Given the opportunity, Collembola can always migrate away from an environment that they find unpleasant (Bengtsson *et al.* 1994a; Krogh 1995a). Nevertheless, the test is useful in highlighting very toxic chemicals, and for assessing the relative toxicities of chemicals to a single species under identical conditions. The *Folsomia candida* test is better than nothing but extreme care must be taken in extrapolating the results to field conditions.

10.2.2 *Biology of Folsomia candida*

Folsomia is a very large genus with more than 100 described species (Appendix A). *Folsomia candida* is among the most intensively studied of all species of Collembola. Aspects of the morphology and biology of *F. candida* have been examined by Bretfeld (1977), Gerdsmeyer and Greven (1989), Goto (1972a), Goto and Ögel (1961), Green (1964) Johnson and Wellington (1980a, 1983), Leonard

and Anderson (1991a), Marshall and Kevan (1962) Palévody (1965), and Van Amelsvoort and Usher (1989a).

Choosing the parthenogenetic species *Folsomia candida* as representative of all Collembola (the 'standard springtail') is about as ecologically sound as choosing a mole as a 'typical' mammal. However, cultures of *F. candida* are very easy to maintain (Hutson 1978b) and their short reproductive cycle at 20°C makes them ideal for conducting laboratory experiments (Kiss and Bakonyi 1990; Spahr 1981). Results from experiments on *F. candida* can not be extrapolated uncritically to other species of Collembola due to differences in sensitivity between species. For example, *F. candida* is highly susceptible to the organophosphorous insecticide fenosulfothion whereas '*Onychiurus justus porteri*' is relatively insensitive (Tomlin 1975). The no observable effect concentration (NOEC) for the herbicide atrazine for *F. candida* is 600 $\mu\text{g g}^{-1}$ (Subagja and Snider 1981) whereas for *Orchesella cincta* it is only 40 $\mu\text{g g}^{-1}$ (Badejo and Van Straalen 1992).

F. candida is a euedaphic springtail with no eyes or pigment. A furca is present and the animal is able to leap a centimetre or so when disturbed. According to the list of world species prepared by Bellinger and Christiansen, *F. candida* has been found in most biogeographic regions of the world except Africa and India. However, many populations are derived from human introductions. The species is often found in caves. In laboratory populations at a constant 21°C, an average female *F. candida* lives for 140 days (maximum 190) and passes through as many as 38 instars (Snider and Butcher 1973). During the early instars, about 20 eggs are laid in each batch but this increases to 100 around the 20th instar before declining back to 60 at the 30th instar (Snider 1973). Eggs are laid in alternate instars. The mean total number of eggs produced by a single female at 21°C is about 1000 although the maximum recorded by Snider and Butcher (1973) was 1654 eggs. Longevity is almost twice as long at 15°C compared with 21°C and egg production is about 30% greater.

Cultures can be maintained on moist plaster of Paris to which a small amount of powdered charcoal or graphite is added at the mixing stage (Booth 1983; Hutson 1978a; Snider *et al.* 1969). This absorbs some metabolic wastes and has the additional advantage of making it much easier to spot the white springtails against the black background. The method adopted in our laboratory is to mix the plaster of Paris powder with water, add the powdered graphite equivalent to about 10% of the volume of the final mixture, and then to pour this into clear plastic sandwich boxes (about 15 cm wide \times 20 cm in length \times 8 cm in depth) to a thickness of about 1 cm. Before the plaster is dry, the surface is scored with a fork creating furrows in which the springtails can lay their eggs. To the naked eye, batches of eggs appear as tiny orange deposits on the edges and on the bottoms of the scored marks. Other culturing techniques have been reported by Aitchison (1986) and Rusek (1978a).

A small amount of dry brewer's or baker's yeast is added in one corner together with a few *F. candida*. These can be readily obtained from cultures in other ecotoxicological laboratories. It is easy to create your own 'strain' by just adding one animal to the box (see Section 8.7). The lid is put on and the containers placed

into a constant temperature room at 20°C. The population builds up quite rapidly so that after a few weeks there will be hundreds of animals in the container. Every couple of months, the majority of adults should be removed to prevent overcrowding and a little more dried yeast added. Some authors have found problems with excessive fungal growth in the cultures (e.g. Goto 1961) but we have never found this to be a problem. Anaesthesia with carbon dioxide is not recommended as this has been shown to reduce fecundity (Goto 1971). At the time of writing, I have maintained cultures of *F. candida* for more than 2 years with no sign of a loss in fecundity; other laboratories have kept cultures of *F. candida* for 5 years or more.

The ease with which *F. candida* can be kept has led to their use in a wide variety of non-ecotoxicological experiments. The species has been employed as a model organism in studies on decomposition and nutrient leaching from leaf litter (Andr  n and Schn  rer 1985; Ineson *et al.* 1982; Naeem *et al.* 1994, 1995), circadian and circaseptan rhythms (Chiba *et al.* 1973; Cutkomp *et al.* 1987*a,b*; Marques *et al.* 1988), the palatability of different species of fungi and leaf litter (Leonard 1984; Schultz 1991; Van Amelsvoort *et al.* 1989*b*), effects of environmental conditions on ageing (Marques *et al.* 1987), grazing of microbes and mycorrhizae (Bakonyi 1989; Warnock *et al.* 1982), and behaviour and population dynamics (Usher and Hider 1975; Usher and Stoneman 1977). Cultures of *F. candida* also provide a convenient source of small prey items for predators such as pseudoscorpions (Johnson and Wellington 1980*b,c*) and mites (Krogh 1995*b*).

10.2.3 The standard test with *Folsomia candida*

The exact details of the standard test vary from laboratory to laboratory but a typical schedule is outlined below. Experiments are conducted at constant temperature (usually 18°C or 20°C) in constant darkness, constant light or a regular light/dark cycle.

The test medium is the artificial soil as recommended for the earthworm standard test by the Organisation for Economic Co-operation and Development (OECD). The soil comprises quartz sand, kaolin clay and *Sphagnum* peat all of which are readily available from builders' merchants, potteries and garden centres respectively. The ingredients are mixed on a weight basis so that the dry soil contains 70% sand, 20% clay and 10% peat. A small amount of powdered calcium carbonate is mixed in to bring the pH up to 6 (the exact quantity determined by trial and error) and distilled water is added so that the final water content is 35% by weight. The test chemicals are incorporated into the soil by adding them in the required concentrations to the water before the soil is hydrated. Lowering the pH and organic matter content of the soil tends to increase the toxicity of chemicals to *F. candida*, especially metals such as cadmium (Crommentuijn 1994).

The test is conducted in small containers (we use plastic vending machine cups) to which soil is added to a depth of about 4 cm. At least four replicates of uncontaminated soil, and each test concentration are prepared. Ten adults are added to each container, preferably from a population in which age and stage of the moult cycle is synchronised (Christian 1988; Crommentuijn *et al.* 1993). Synchrony is

achieved by allowing adult *F. candida* to oviposit into a fresh culture vessel and then removing them after 2 days. After 2 weeks, the eggs hatch and the juveniles are allowed to feed on dried yeast for 7 days by which time they are all of the same size and are ready to be introduced into the test containers.

Ten *F. candida* are placed into each cup together with a small amount of dried yeast. These containers are then left for a minimum of three weeks by which time the surviving females will have matured and laid eggs. The soil is flooded with distilled water and the adult springtails and their offspring float to the surface. Each container is photographed from above onto transparency film. When developed, the slides are projected onto a viewing screen and the total number of adults and offspring are counted (Fig. 10.2). The position of each springtail is marked on a transparent overlay which facilitates accurate counting.

The adults can be removed after photography, and weighed and analysed to determine the concentrations of the test chemical in their bodies. If large numbers of replicates are prepared, then batches of these are flooded at intervals to allow calculation of survival, growth and reproduction with time. NOECs are determined, or other toxicity values such as the concentration of the chemical causing a 50% reduction in growth, juvenile production and adult survival compared to controls. The latter values are known as EC₅₀s. The results from a comprehensive experiment on the effects of cadmium on *F. candida* by Crommentuijn *et al.* (1993) are shown in Tables 10.1 and 10.2, and Fig. 10.3.

Interclonal variation in *F. candida* is not large (Crommentuijn 1994). The test is easy to carry out, it requires little attention while it is running, and it gives reproducible results (Van Straalen and Van Gestel 1993). The only disadvantage of the test is that reproduction cannot be observed directly, and cannot be separated from juvenile mortality and hatching success. Reproduction depends largely on the body size of the adults, so any chemical that inhibits growth will also reduce the number of offspring recovered (Van Gestel and Van Straalen 1994). The latter was the main effect of cadmium on *F. candida* in the experiments of Crommentuijn *et al.* (1993).

Table 10.1. Estimates of median effect concentrations for survival, number of offspring and body weight for *Folsomia candida* exposed to cadmium in artificial soil. Reproduced from Crommentuijn *et al.* (1993) by kind permission of the authors and Academic Press.

Days of exposure	LC ₅₀ ($\mu\text{g Cd g}^{-1}$ dry soil)	95% Confidence range	EC ₅₀ offspring ($\mu\text{g Cd g}^{-1}$ dry soil)	95% Confidence range	EC ₅₀ weight ($\mu\text{g Cd g}^{-1}$ dry soil)	95% Confidence range
19	917	708–1187			448	393–512
23	778	684–889	159	131–192	376	332–426
26	822	424–1595	204	161–258	566	501–639
30	893	736–1085	227	184–279	541	486–604
35	854	604–1208	>326		807	733–888
42			>326			

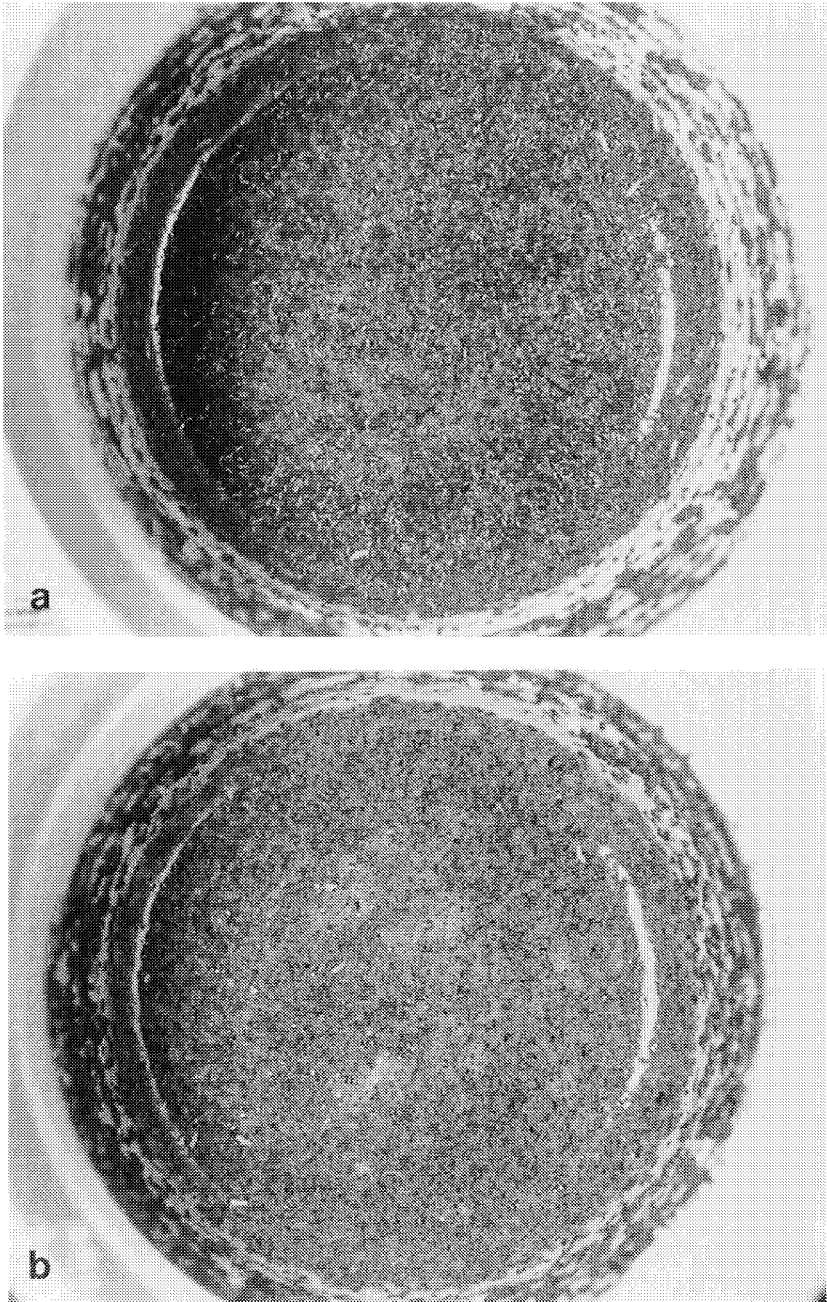


Fig. 10.2. Photographs from above of *Folsomia candida* floating on the surface of water added to artificial soil, 3 weeks after 10 adults were placed in each container. The control (a) contains many hundreds of juveniles. However, the soil to which lead was added (b) at a concentration of $10\,000\ \mu\text{g Pb g}^{-1}$ contains only a few surviving adults which have not bred. The diameter of each container is 6 cm. Photographs by Steve Hopkin.

Table 10.2. Estimates of median effect concentrations for survival on day 35, number of offspring and body weight on day 35, Von Bertalanffy growth, and population increase for *Folsomia candida* exposed to cadmium in artificial soil. Reproduced from Crommentuijn *et al.* (1993) by kind permission of the authors and Academic Press.

Parameter	EC ₅₀ ($\mu\text{g Cd g}^{-1}$ dry soil)	95% Confidence range
Survival day 35	854	604–1208
Offspring day 35	>326	
Body weight day 35	807	733–888
Growth rate	256	223–293
Population increase	475	411–549

Recent advances in computer technology have allowed the behaviour of individual *F. candida* to be monitored in response to test chemicals (Sorensen *et al.* 1995). However, such results are difficult to relate to effects at the population level.

10.2.4 Effects of chemicals on other species of *Collembola*

A number of other species have been used in laboratory tests but very few have reached the stage of being as routine as *F. candida*. The favoured species of a research group at Lund University in Sweden is *Protaphorura armata* which has been exposed to chemicals via a fungal diet (see Bengtsson *et al.* 1985*b*; Tranvik *et al.* 1993). *Orchesella cincta* is employed extensively by a research group based at the Free University, Amsterdam where the species has been maintained in culture for several years. Toxicity tests are conducted on individual animals and the chemicals (mainly metals) have been administered via the food in contaminated algae (see Appendix C). Because *O. cincta* reproduces sexually, it is possible to perform genetic experiments by selecting particular spermatophores from known males and allowing specific females to pick these up (Posthuma and Janssen 1995; Posthuma *et al.* 1992, 1993*a,b*).

These and other studies have been important in demonstrating that responses to chemicals are species-specific. The *F. candida* test is a useful first step but the use of further species is to be encouraged so that a broader view of the toxicity of chemicals to *Collembola* can be obtained.

10.3 Risk assessment

There has been considerable discussion on the legitimacy of using NOECs, LC₅₀s and other parameters for quantifying the effects of chemicals on test species (see e.g. Laskowski 1995; Van Straalen *et al.* 1994; Van Wensem *et al.* 1994). A recent discussion of this topic by Chapman *et al.* (1996) concluded that the most appropriate value to use for regulatory purposes is the EC₅₀ which is the concentration of a chemical that affects 50% of the test organisms during the test period. There was much less interlaboratory variation between EC₅₀s than between NOECs

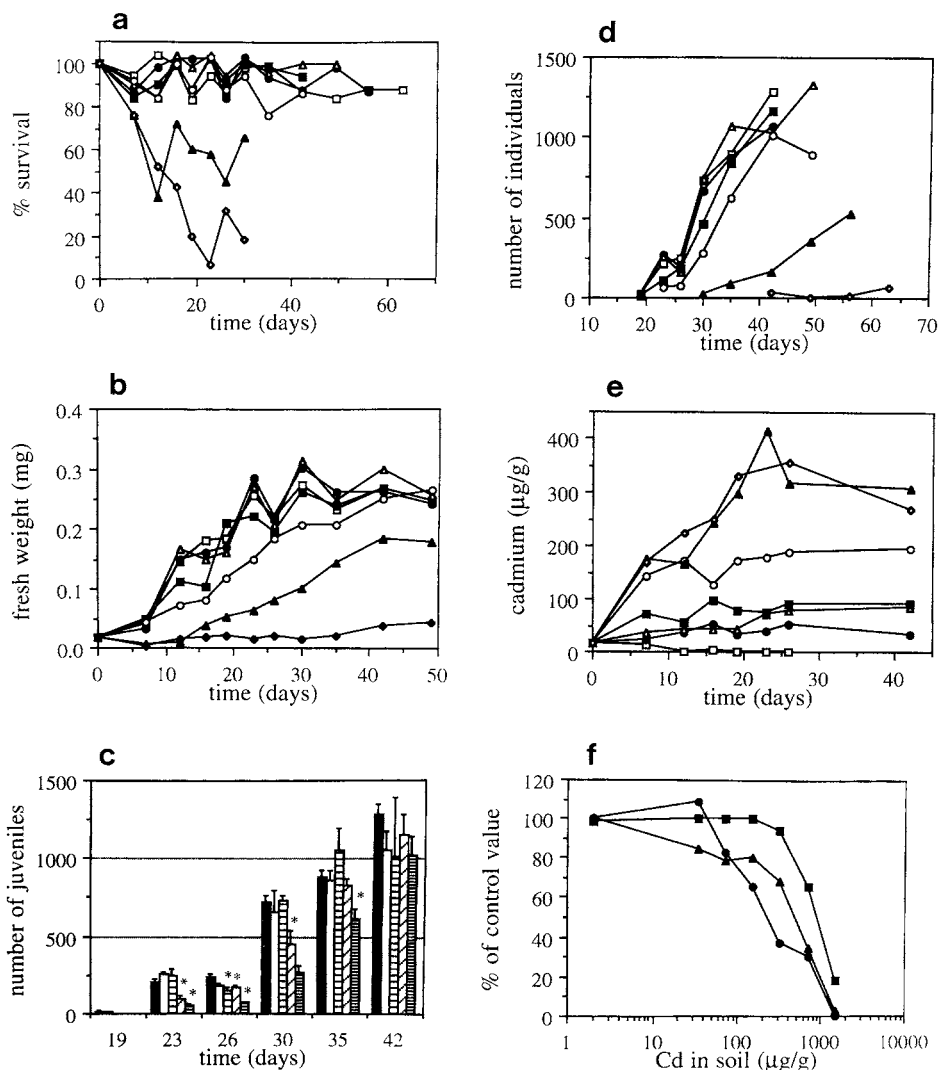


Fig. 10.3. Results of a laboratory test on the toxicity of cadmium to *Folsomia candida* in artificial soil. (a) Percentage survival (empty squares = control, filled circles = $34.8 \mu\text{g g}^{-1}$, empty triangles = $71.3 \mu\text{g g}^{-1}$, filled squares = $148 \mu\text{g g}^{-1}$, empty circles = $326 \mu\text{g g}^{-1}$, filled triangles = $707 \mu\text{g g}^{-1}$, empty diamonds = $1491 \mu\text{g g}^{-1}$. Survival calculated from the number of adults present in the containers sacrificed independently at various times. (b) Growth of adults expressed in mg fresh weight (for definition of symbols see a). (c) Mean number of juveniles at different sampling dates (bars = standard error; solid bars = control, empty bars = $34.8 \mu\text{g g}^{-1}$, wide horizontal shading = $71.3 \mu\text{g g}^{-1}$, diagonal shading = $148 \mu\text{g g}^{-1}$, close horizontal shading = $326 \mu\text{g g}^{-1}$. The concentrations for which the number of offspring was significantly lower than the control are marked with an asterisk (Williams test, $p < 0.05$). (d) Total number of individuals (for definition of symbols see a). (e) Accumulation of cadmium ($\mu\text{g g}^{-1}$ dry weight) (for definition of symbols see a). (f) Dose-effect relationships for survival at day 35 (filled squares), Von Bertalanffy growth (filled circles) and population increase (filled triangles). The values at the different concentrations are expressed as the percentage of the control values. Reproduced from Crommentuijn *et al.* (1993) by kind permission of the authors and Academic Press.

when the results from the same tests were compared. However, in the absence of a consensus on this issue, the discussion of risk assessment below will be kept fairly broad.

Virtually all environmental contaminants can be found everywhere if the analyst looks hard enough and has a sufficiently sensitive instrument (Mackay 1988). The role of the ecotoxicologist is to suggest 'safe' environmental concentrations of chemicals which provide the least possible disruption of ecosystem processes. The main problem encountered is relating dose-response curves derived from laboratory experiments to field conditions where climatic conditions are variable and bioavailability of chemicals may be very different (Van Wensem *et al.* 1994). A widely used approach is to incorporate a safety factor and divide the EC_{50} or NOEC for the chemical by 10 (or, if one wants to be really conservative, by 100) to give the maximum acceptable environmental concentration.

However, it is clear that in modern industrial societies, the target of 100% protection is not likely to be achieved. Many chemicals are used with the deliberate purpose of killing pests and it is inevitable that non-target species will be affected. One approach developed by scientists mainly in The Netherlands is to accept that it may never be possible to protect all organisms, but that one should aim to protect 95% of species (Aldenberg and Slob 1993; Van Straalen 1993a; Van Straalen and Denneman 1989). The level of a chemical which affects only 5% of species is known as the HC_5 (hazardous concentration for 5% of species). The HC_5 approach assumes that the relationship between the number of species (y axis) and the \log_{10} NOEC of a chemical (x axis) for each species is described by a normal distribution. The HC_5 value is the level in soil at which 95% of species will theoretically be unaffected (Fig. 10.4).

However, there are a number of problems with the HC_5 approach, mainly concerned with the small number of experiments on which the values are based, and extrapolation of laboratory results to the field (see Hopkin 1993a and reply by Van Straalen 1993b). For example, Badejo and Van Straalen (1992) proposed an HC_5 value of $2.7 \mu\text{g g}^{-1}$ for atrazine that would protect 95% of soil invertebrates,

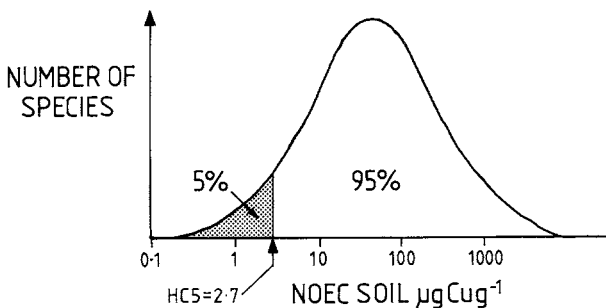


Fig. 10.4. Schematic diagram of the proposed relationship between number of species and No Observed Effect Concentration (NOEC) of copper for soil invertebrates. Van Straalen (1993a) has suggested that the hazardous concentration below which 5% of species are affected by copper poisoning (HC_5) may be only $2.7 \mu\text{g g}^{-1}$. Reproduced by kind permission of the *Oikos* Editorial Board, Lund, Sweden.

but this was based on experiments on only five species (four of them Collembola). Large differences in toxicities of chemicals to different species are the rule rather than the exception (Van Straalen 1994b). Toxicity of chemicals in laboratory experiments is invariably greater than in the field so that harmful levels will be overestimated and HC_5 values will be correspondingly too low (Van Wensem *et al.* 1994). It is also assumed that the curve shown in Fig. 10.4 is symmetrical. In the field, it is far more likely that the curve to the left of the peak is truncated and for copper, cuts through the x axis around the $10 \mu\text{g g}^{-1}$ mark. Indeed the HC_5 value for copper of $2.7 \mu\text{g g}^{-1}$ as reported by Van Straalen (1993a) is nearly half the concentration below which a soil is regarded as copper deficient for agriculture ($5 \mu\text{g g}^{-1}$). It is unlikely that organisms would be poisoned at such a low level of copper (Hopkin 1993a).

Determination of NOECs from chronic reproduction experiments on standard test species provides a useful assessment of the relative toxicities of chemicals and are potentially useful for the study of synergistic and antagonistic effects (Van Straalen *et al.* 1994). However, direct laboratory to field extrapolation of standard test results for long-term risk assessment is not legitimate (Filser and Nagel 1993). Long-term effects at the population level are assessed most satisfactorily in outdoor conditions.

10.4 Effects of chemicals on Collembola in the field

Much concern has been expressed regarding effects of pesticides and pollutants on Collembola in the field (Frampton 1994). Several authors have proposed that the abundance, species diversity and life history characteristics of Collembola can provide information on the impact on ecosystems of chemicals, or particular management strategies (Filser 1995a; Greenslade and Greenslade 1987; Hogervorst *et al.* 1993; Kopeszki 1991, 1992a,b, 1993a,b; Reddy 1986; Siepel 1995; Stork and Eggleton 1992; Van Straalen *et al.* 1988).

Chemicals may affect total abundance of Collembola, species diversity, and presence or absence of particular species and their dominance. Pooling samples of 'microarthropods' (Colinas *et al.* 1994), or total Collembola (Hopkin *et al.* 1985; Hunter *et al.* 1987) is to be discouraged because important effects on the relative abundances of different species cannot be resolved. Studies at the species level require sound taxonomy. Synonymy and disagreements over the boundaries of biological species are impediments to between-site comparisons of pollution impact, especially if these are in different biogeographical regions (Hopkin *in press*).

A decrease in the number of Collembola in a habitat after it has been sprayed with insecticides is often the result of direct toxicity. However, reduced numbers may be caused by indirect effects. For example, the fungicide Aktuan reduces populations of fungal feeders such as *Hypogastrura assimilis* by killing their hyphal food (Filser 1994).

It might be assumed that pollution would decrease populations of all species of Collembola but this is not necessarily the case. Indeed, a common response at intermediate levels of pollution or pesticide application is for numbers of certain

species to increase (Czarnecki and Losinski 1985; Frampton *et al.* 1992; Moore *et al.* 1984; Wilson *et al.* 1995). The effect may be indirect due to removal of predators such as mesostigmatid mites which are more sensitive to the chemical (Edwards *et al.* 1967). Preferred species of fungus may also grow better, and some species of Collembola benefit from reduced competition from less tolerant species of springtail (Hågvar 1990). Hopkin *et al.* (1985) found higher total numbers of Collembola in a woodland heavily contaminated with aerial metal pollution than in a control site. They concluded that the thick layer of leaf litter, which had accumulated due to the lack of earthworms, favoured the Collembola by providing a greater volume of stable habitat.

Some species of Collembola can be regarded as 'acidophilic' and others as 'calciophilic'; acid rain or liming will favour the former or latter species respectively (Hågvar 1987*a,b*; Hagvår and Kjøndal 1981*b*; Rusek 1993). *Isotoma notabilis* seems to be particularly susceptible to acid rain (Hågvar 1984). Hagvår and Abrahamsen (1990) determined the abundances of different species of Collembola along a natural gradient of lead contamination in Norway. *Isotoma olivacea* reached its highest density at an intermediate point on the gradient above which the normally abundant *Protaphorura armata* was much less numerous (Fig. 10.5).

Bengtsson and Rundgren (1988) studied the soil fauna along a gradient of metal pollution near Gusum in Sweden and found that populations of Collembola peaked at intermediate levels of pollution (Fig. 10.6). Differences in sensitivity between species were noted. *Isotomiella minor* and *Folsomia quadrioculata* were relatively less abundant near the source of contamination than *Folsomia fimetariodes* which demonstrated an increase in relative numbers compared to uncontaminated sites (Fig. 10.7). In laboratory experiments, Tranvik and Eijsackers (1989) showed that *F. fimetariodes* had a higher preference for metal tolerant fungi than *I. minor*. When given the choice between polluted and unpolluted fungi, *F. fimetariodes* significantly avoided the contaminated food whereas *I. minor* did not. Thus the availability of its preferred fungal species, and a better ability to avoid metals, favours *F. fimetariodes* and explains its dominance over *I. minor* in polluted soils (Fig. 10.7).

Thus in response to contamination, some species move away, some are killed and others increase their abundance. We could predict that *Folsomia quadrioculata* (which often accounts for more than 40% of individual Collembola in temperate habitats; Gerdsmeyer and Greven 1987, 1992), is likely to be reduced in numbers as it appears to be quite sensitive to chemicals (Filser *et al.* 1995; Tranvik and Eijsackers 1989). The sensitivity of *I. minor* to a variety of environmental contaminants has also been noted by Filser *et al.* (1995) and Kopeszki (1993*a*). However, the detailed responses of every species are very difficult to predict.

Hågvar (1994) proposed a simple model which takes account of the above difficulties by recommending the use of dominance values. Natural stable communities are generally characterised by having many rare species and a few abundant ones (e.g. Fig. 9.8). If individuals per species are presented on a logarithmic scale,

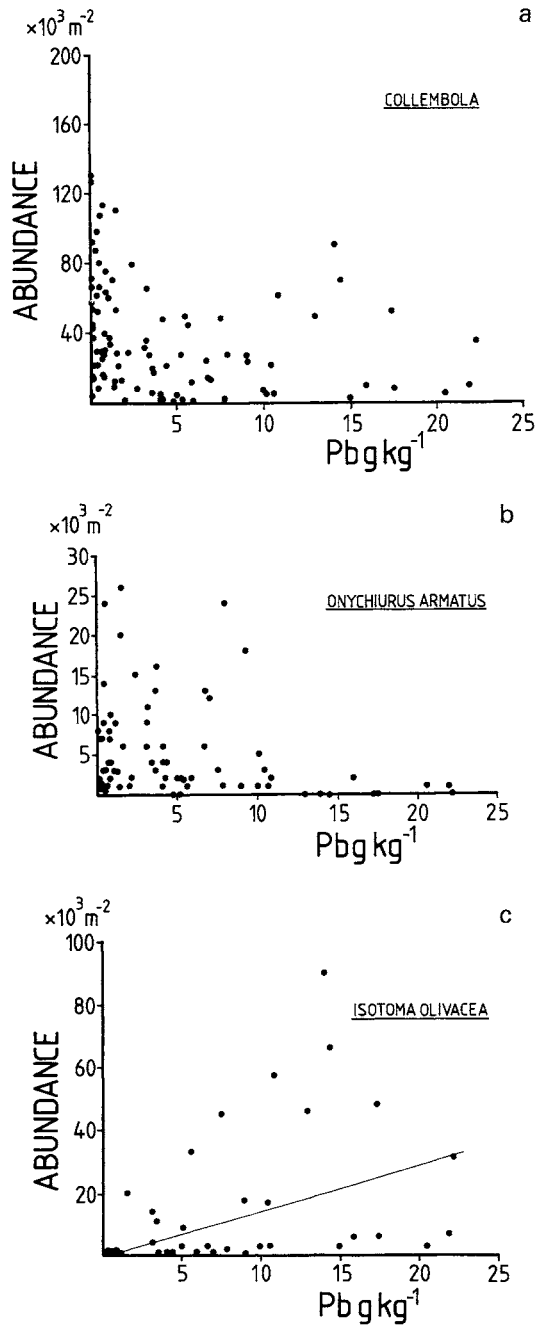


Fig. 10.5. Abundance of (a) total Collembola, (b) *Onychiurus armatus* (= *Protaphorura armata*) (Onychiuridae) and (c) *Isotoma olivacea* (Isotomidae) in the 0–3 cm layer in lead-contaminated soils in the vicinity of a natural metalliferous outcrop in a Norwegian spruce forest. The concentrations of lead represent metal extracted from soil over 18 h in 0.1 M buffered acetic acid. Note that *O. armatus* is sensitive to lead pollution whereas *I. olivacea* reaches higher population densities in contaminated soils. Redrawn from Hågvar and Abrahamsen (1990) by kind permission of the authors and the Entomological Society of America.

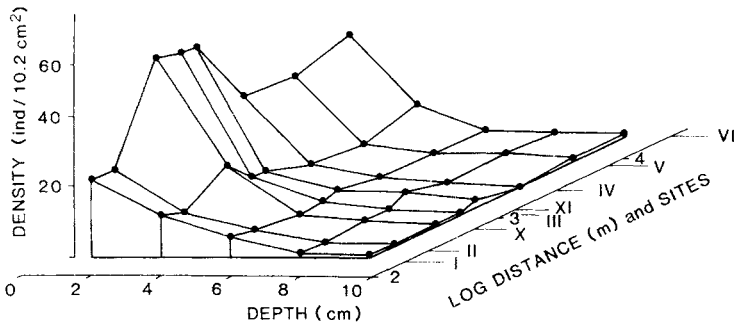


Fig. 10.6. Density of Collembola at different depths in coniferous forest soils contaminated with copper and zinc at different distances from a brass mill at Gusum, Sweden. Reproduced from Bengtsson and Rundgren (1988) by kind permission of the authors and the National Research Council of Canada.

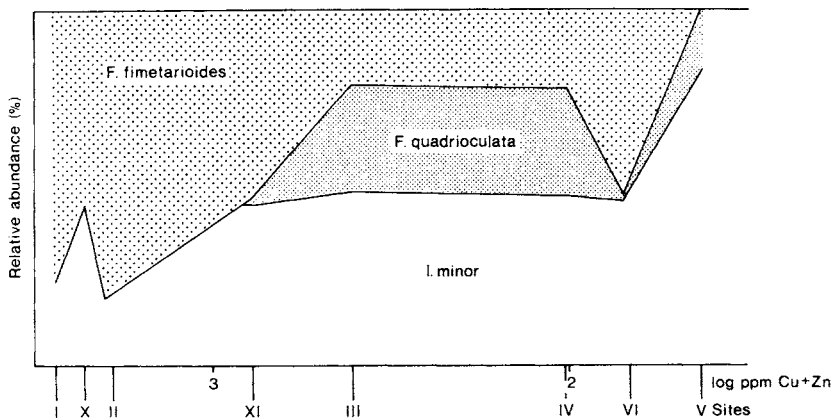


Fig. 10.7. Relative abundances of *Folsomia fimetarioides*, *Folsomia quadrioculata* and *Isotomiella minor* (Isotomidae) in soils at Gusum (cf. Fig. 10.6). Reproduced from Bengtsson and Rundgren (1988) by kind permission of the authors and the National Research Council of Canada.

the species numbers are usually distributed normally giving a 'log normal' distribution. In most communities under pollution stress, certain species become very abundant and the curve is distorted. However, Hågvær (1994) showed that stressed communities of Collembola rarely show extreme high densities of certain species. He therefore proposed using the log normal distribution of *dominance values* as a reference (Fig. 10.8). These changes in the dominance structure could be used as an 'early warning' criterion for stressed communities. Under such stress, rare species may increase their abundances and perform important ecosystem processes that would normally be carried out by the dominant species (decomposition etc.).

Laboratory standard tests are generally reproducible and easy to carry out. Field studies are labour-intensive but they provide essential information on the real effects of chemicals on natural populations. However, it is difficult to compare

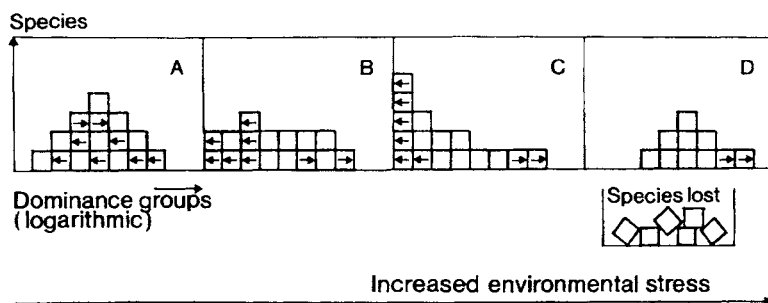


Fig. 10.8. A model for changes in the dominance structure of a community under increased environmental stress. 'Sensible' species (Hågvar's terminology) move to lower dominance classes, while 'tolerant' species increase their dominance. The original, stable log-normal distribution (A) is flattened out (B) and then skewed to the left (C). After the 'sensible' species have been lost, a new log-normal distribution may appear (D). Reproduced from Hågvar (1994) by kind permission of the author and the Finnish Zoological and Botanical Publishing Board.

results derived from these two approaches. A possible compromise is to conduct tests in microcosms where small 'parcels' of habitat containing groups of Collembola are maintained in conditions which bear some similarity to the natural environment (Filser and Nagel 1993; Hågvar 1988; Parmelee *et al.* 1993; Teuben and Verhoef 1992a). For example, Wiles and Frampton (1996) assessed the effects of three pesticides on four species of Collembola by removing soil from fields that had been sprayed and then exposing four species of Collembola to the soil in the laboratory (Figs. 10.9–10.11). Such an approach allows the relative toxicities of chemicals to species to be determined simultaneously and enables the influence of soil type and spraying regime (with or without crops) on the performance of Collembola to be assessed.

10.5 Assimilation of chemicals by Collembola

Many modern pesticides have short half-lives in the environment. Their main effects on Collembola are due to direct toxicity from contact poisoning, or starvation if fungicides are applied which wipe out their food. However, there are some chemicals which are persistent and potentially dangerous because they resist breakdown into less harmful components. This is particularly true of metals, which will be highlighted here as an example of how Collembola deal with such chemicals.

Metal pollutants are derived from smelting and mining activities, fossil fuel burning and deliberate application as pesticides. Copper, for example, is still used extensively for controlling fungal diseases of coffee plants and grape vines. These elements pass along food chains. Organisms have evolved a variety of mechanisms to prevent intracellular concentrations of soluble metals from interfering with essential biochemical processes in tissues. Fungivorous Collembola are particularly vulnerable to exposure to metals and radioactive isotopes in their diets because the hyphae accumulate elements to concentrations which are an order of

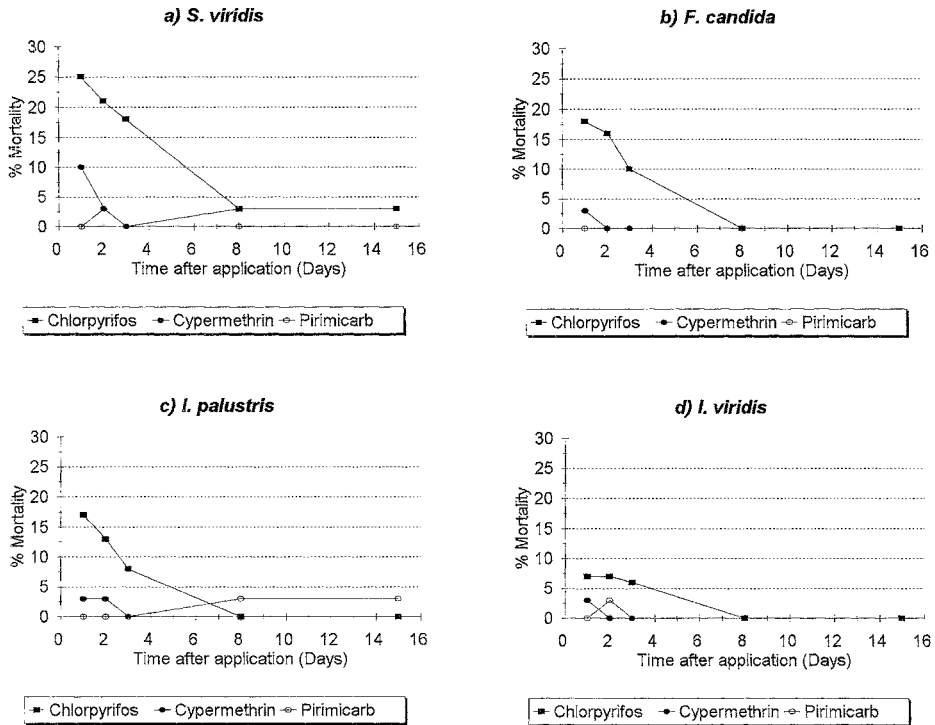


Fig. 10.9. The toxicity of chlorpyrifos, cypermethrin and pirimicarb to (a) *Sminthurus viridis* (Sminthuridae), (b) *Folsomia candida* (Isotomidae), (c) *Isotomurus palustris* (Isotomidae) and (d) *Isotoma viridis* (Isotomidae) on a sandy clay loam soil under a cereal crop canopy sprayed in the field then brought into the laboratory for testing. All data corrected for control mortality. Reproduced from Wiles and Frampton (1996) by kind permission of the authors and John Wiley.

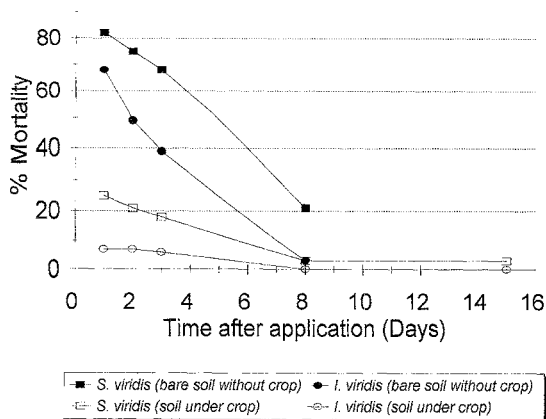


Fig. 10.10. The toxicity of chlorpyrifos residues to *Sminthurus viridis* and *Isotoma viridis* on a sandy clay loam soil in the presence and absence of a cereal crop canopy sprayed in the field then brought into the laboratory for testing. All data corrected for control mortality. Reproduced from Wiles and Frampton (1996) by kind permission of the authors and John Wiley.

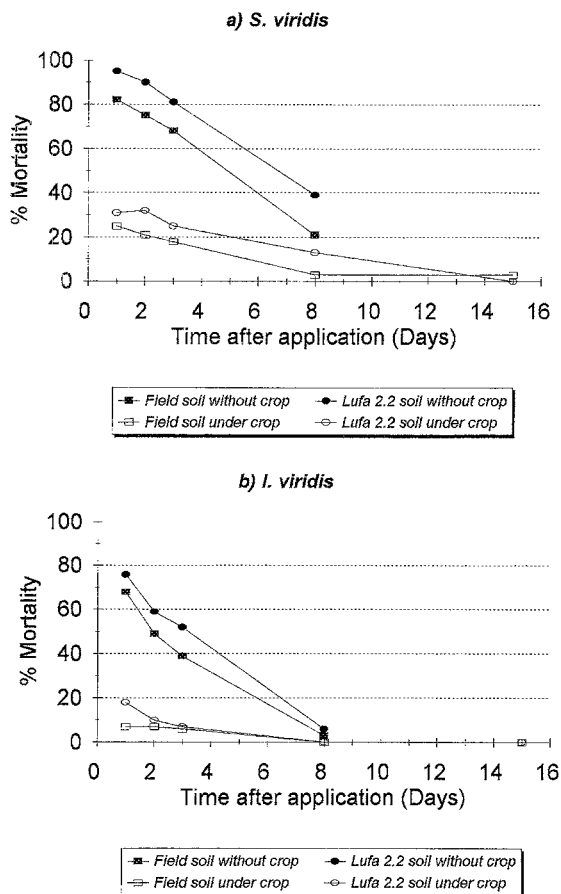


Fig. 10.11. The toxicity of chlorpyrifos residues to *Sminthurus viridis* and *Isotoma viridis* on two different soils in the presence and absence of a cereal crop canopy sprayed in the field then brought into the laboratory for testing. All data corrected for control mortality. Reproduced from Wiles and Frampton (1996) by kind permission of the authors and John Wiley.

magnitude or more higher than the levels in the surrounding soil (Bååth 1991; Borio *et al.* 1991; Brückmann and Wolters 1994; Hopkin 1994; Hove *et al.* 1990). Collembola are subject to high levels of predation (Van Straalen and De Goede 1987), so the [fungus → springtail → predator] food chain is an important critical pathway for many pollutants in terrestrial ecosystems (Van Straalen *et al.* 1985).

Bioaccumulation in organisms may enhance the persistence of industrial chemicals in the ecosystem as a whole by fixation in the tissues of organisms (Streit 1992). In Collembola, metals tend to be present in two compartments in the body from which they are lost at different rates (Fig. 10.12). One compartment contains metals present throughout the body tissues which take some time to be excreted when loading ceases (slow component). The second compartment is the digestive

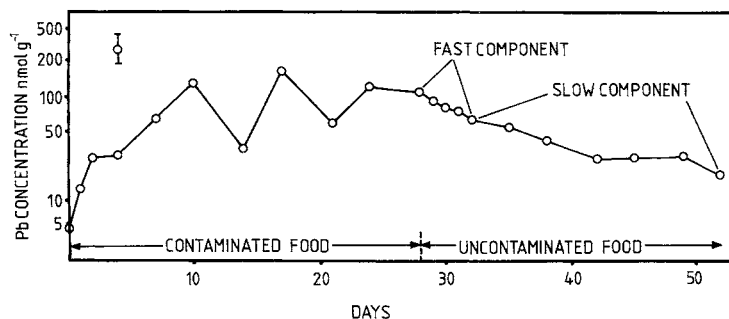


Fig. 10.12. Concentration of lead in *Orchesella cincta* (Entomobryidae) fed on a suspension of the green alga *Pleurococcus* sp. containing $2000 \mu\text{g Pb g}^{-1}$ for 28 days followed by uncontaminated food. Each mean is based on five replicate observations of two pooled individuals. Each mean has a standard error as shown in the upper left corner. Lead in gut contents was excluded from the concentration determinations. There are two components to loss of assimilated lead from the tissues. The fast phase probably represents loss via exfoliation of the intestinal epithelium whereas the slow component represents lead which has accumulated in the rest of the body tissues and is more difficult to excrete. Redrawn from Van Straalen and Van Meerendonk (1987) by kind permission of the authors and Springer-Verlag.

epithelium (fast component) which acts as a site of storage detoxification of metals bound in insoluble granules (Humbert 1980, 1981; Humbert and Barra 1979; Fig. 4.16). Such granules can be found in most invertebrate digestive epithelia and are the most common method of storage detoxification of a wide variety of unwanted essential and non essential metals (for reviews see Beeby 1991; Dallinger 1993; Hopkin 1989, 1990, 1995; Hopkin *et al.* 1989). In Collembola, the granules are lost in the faeces when the lining of the gut is excreted during moulting (Joosse and Verhoef 1983). The system is a very effective way of ridding the animals of unwanted substances (Pawert *et al.* 1996; Van Straalen and Van Meerendonk 1987).

Predators of organisms which have accumulated harmful substances may be endangered by food chain effects if they are unable to switch to a less contaminated diet. For example, the pooled samples of Collembola (mostly *Orchesella villosa*) collected from a site adjacent to a copper refinery near Liverpool, UK by Hunter *et al.* (1987) had whole body concentrations of $2370 \mu\text{g Cu g}^{-1}$ dry weight (compared to a value of $49.5 \mu\text{g Cu g}^{-1}$ in control samples). Apart from terrestrial isopods ($2390 \mu\text{g Cu g}^{-1}$ dry weight), the springtails contained the highest levels of copper found in any detritivorous invertebrate. Although these Collembola would have been able to excrete much of this copper the next time they moulted, the springtail population provided a substantial source of metal for their predators.

A metal does not need to be 'biomagnified' for it to be a danger to predators (Roth 1993; Streit 1992). What is important are the levels which are toxic to predators, not whether the springtail contains more of a particular substance than is in its food (Janssen and Hogervorst 1993; Janssen *et al.* 1993; Laskowski 1991; Van Straalen 1987; Van Straalen and Ernst 1991). Predators which specialise on Collembola, such as the carabid beetle *Leistus sardous* (see Fig. 7.6), are

vulnerable to poisoning in contaminated sites if they do not possess effective detoxification mechanisms to cope with a continuous influx of metals.

The extent of bioaccumulation of chemicals in Collembola may differ substantially between species (Van Straalen and Van Wensem 1986). In central Italy, for example, a study by Lupetti *et al.* (1994) showed that *Orchesella cincta* contained concentrations of DDTs and PCBs about six times higher than those observed in *Orchesella villosa* which, in turn, contained levels five times higher than in *Tomocerus minor*. This phenomenon can be explained by species-specific differences in the balance between assimilation and excretion (and for some organic chemicals, the rate of breakdown in the tissues). In *O. cincta* for example, the efficiency of assimilation of lead and cadmium from a contaminated algal diet was 0.4% and 8.3% respectively (Van Straalen *et al.* 1987). Of the assimilated metals, 48% of the lead and 30% of the cadmium was excreted at each moult through loss of the intestinal epithelium. This explains why the concentration factor (concentration of metal in *O. cincta*/concentration of metal in food) for cadmium is higher than that for lead. In the field, differences in the concentrations of chemicals in preferred diets may enhance such species-specific differences.

10.6 Evolution of genetic resistance to chemicals

Collembola are one of the few groups of terrestrial invertebrates in which genetically based tolerance to metals (here called *resistance*) has definitely been demonstrated (for a review of all aspects of this topic, see Posthuma and Van Straalen 1993). As far as I am aware, resistance to organic chemicals has not been demonstrated in springtails. In *Drosophila melanogaster*, resistance to cadmium and copper is due to duplication of the gene coding for the metal-binding protein metallothionein (Maroni *et al.* 1987). Metallothionein proteins have yet to be found in Collembola, although they are probably present.

Resistance to metals in Collembola is of a degree, not of a kind. In other words, it involves the enhancement of existing mechanisms such as storage detoxification and excretion rather than completely novel phenomena. The main mechanism of resistance to cadmium and lead in populations of *Orchesella cincta* from contaminated sites is increased efficiency of excretion of assimilated metals during loss of the gut epithelium at moult (Posthuma *et al.* 1992, 1993a; Van Straalen *et al.* 1986). However, resistant populations tolerate higher concentrations of cadmium in their diet (Posthuma 1990) and females from contaminated sites tend to reproduce at an earlier age than females from control populations; the immediate post-hatching body weight of juveniles also tends to be larger in resistant populations (Posthuma *et al.* 1993b). Similar effects on life history characteristics of *Protaphorura armata* and *Isotoma notabilis* from metal-contaminated sites were found by Tranvik *et al.* (1993).

Frati *et al.* (1992a) reported a correlation between the frequency of alleles for glutamate-oxaloacetate transaminase (*Got*) and cadmium tolerance in *O. cincta* from various polluted sites. In *Orchesella bifasciata* however, such correlations could not be found for the frequencies of alleles of two enzymes (*Pgi* and *Pgm*)

along a transect away from the Gusum brass mill in Sweden (Tranvik *et al.* 1994). Thus, the role of specific *Got* alleles in metal tolerance in *O. cincta* remains to be established (Posthuma and Van Straalen 1993).

The genetic diversity for life history characteristics such as growth rate and clutch size is sufficient in unstressed populations for selection for these characters to take place in metal-stressed environments (Posthuma and Janssen 1995). However, near point sources, pollution gradients are steep and there is a high degree of genetic mixing which mitigates against the evolution of distinct, reproductively isolated, metal-resistant strains (Tranvik *et al.* 1994). Thus although some species of Collembola can evolve a degree of resistance to metals, this does not convey a massive advantage over species like *Isotoma olivacea* (see Fig. 10.5) and *Folsomia fimetariodes* (see Fig. 10.7) which are apparently 'pre-adapted' to succeed in contaminated environments.

10.7 Conclusions

The *Folsomia candida* standard test provides a simple and reproducible method for measuring the absolute and relative toxicities of existing and new chemicals to non-target species of soil invertebrates. The test is also potentially useful for studying antagonistic and synergistic effects between chemicals but very little work of this type has been carried out. However, results of the test cannot be extrapolated uncritically to the field due to species-specific differences in sensitivities to chemicals and variations in bioavailabilities of chemicals under field conditions.

The HC₅ approach to risk assessment shows promise but many more experiments are required on a wider range of species of Collembola before the relationship shown in Fig. 10.4 can be confirmed (Van Straalen *et al.* 1994). In addition, the left-hand part of the curve should not be extrapolated below the lowest NOEC value determined in a laboratory experiment. The use of microcosms for studying pesticide effects is to be encouraged as these provide a useful compromise between the simplicity of the *F. candida* test and the complexity of the field (Filser and Nagel 1993; Wiles and Frampton, 1996). The predictive nature of tests could be improved with further knowledge of the biochemical basis of the effects of particular chemicals on Collembola.

Mathes and Weidemann (1990) stated that the 'real ecotoxicologist, who produces a practical toxicological method with true ecosystem-level end points and reliable predictive power does not exist'. Complete prediction of the effects of chemicals, or different management strategies, on natural populations of Collembola is an unachievable goal but we could certainly get closer by long-term, before and after monitoring of impacted sites (Dunger 1991a; Filser 1991, 1995a). The broad approach of authors such as Hågvar (1994) is also to be encouraged as this provides hypotheses which can be tested in real ecosystems.

Appendix A

World genera of Collembola

This list is based on the comprehensive table of genera and species circulated electronically on the Internet by Peter Bellinger and Ken Christiansen. I am very grateful for their permission to base Appendix A on their work. The number of species (spp.) included in their list as at September 1995 (with a few minor amendments) is given for each genus. If the authorities for genera (immediately after each genus name) are not included in the alphabetical lists of Ellis and Bellinger (1973, 1984), they are given in *italics* and the full citation is included in the reference list at the end of this book. For some genera, I have cited recent publications in which the genus has been revised, or new species have been described.

A few changes have been made to the electronic list in response to comments by Louis Deharveng, Arne Fjellberg and Penny Greenslade. In particular, some Subfamilies have been raised to Family level. However, I have retained the Sminthuridae as a Family for the moment as there is some disagreement as to the status of the various Subfamilies in this group. My own view is that the category of subgenus is confusing, particularly for the beginner and that subgenera (where well defined as monophyletic units) should be raised to generic status. For example in Onychiurinae, *Protaphorura*, *Hymenaphorura* etc. (considered by some as subgenera of *Onychiurus*) are treated as genera.

Isotomidae is not divided into Subfamilies here as there is some disagreement on their validity as monophyletic units when the world fauna is considered. I have also omitted Tribes from the list. Some are well defined but others are controversial so I decided on balance to leave them out.

Finally, I would emphasise that the arrangement as presented here is not definitive. Genera are arranged in their most likely monophyletic groupings in an accessible form which will allow readers to locate literature on particular taxa. For example, presentation of the Sminthuridae as a Family is not meant to imply that Betsch (1980) is wrong, and that Richards (1968) is correct, merely that where there is disagreement, I have erred towards the conservative rather than the radical view.

Class COLLEMBOLA

1 Order ARTHROPLEONA

1.1 Superfamily Poduroidea (= Poduromorpha)

1.1.1 Family BRACHYSTOMELLIDAE (96 spp.)

1. Bonetella Stach, 1949 (1sp.)

2. **Brachystomella** Ågren, 1903 (61sp.) (see Christiansen and Bellinger 1992; Greenslade and Najt 1987a; Mendonca and Arlé 1992; Najt and Thibaud 1988; Najt *et al.* 1991; Thibaud and Najt 1993; Weiner and Najt 1991b)
3. **Brachystomellides** Arlé, 1959 (4 spp.)
4. **Cassagnella** Najt and Massoud, 1974 (2 spp.)
5. **Folsomiella** Bonet, 1930 (5 spp.)
6. **Micronella** Arlé, 1959 (2 spp.)
7. **Parastomella** Rapoport and Rubio, 1968 (1 sp.)
8. **Probrachystomellides** Weiner and Najt, 1991b (1 sp.)
9. **Raponella** Najt, 1988 (1 sp.)
10. **Rapoportella** Ellis and Bellinger, 1973 (1 sp.) (see Greenslade and Najt 1987a; Najt and Palacios-Vargas 1986)
11. **Salvarella** Greenslade and Najt, 1987b (1 sp.)
12. **Setanodosa** Salmon, 1942 (13 spp.) (see Christiansen and Bellinger 1992)
13. **Subclavontella** Stach, 1949 (2 spp.)
14. **Winterella** Massoud, 1967 (1sp.)

1.1.2 Family HYPOGASTRURIDAE

1.1.2.1 Subfamily GULGASTRURINAE (1 sp.)

1. **Gulgastrura** Yosii, 1966 (1 sp.) (see Lee and Kim 1995a; Lee and Thibaud 1987)

1.1.2.2 Subfamily HYPOGASTRURINAE (577 spp.)

(see Babenko *et al.* 1994 for numerous new species in this subfamily)

1. **Acherongia** Massoud and Thibaud, 1985 (3 spp.) (see Fjellberg 1991e)
2. **Acherontides** Bonet, 1945 (8 spp.) (see Deharveng and Diaz 1984; Palacios-Vargas and Gnaspini-Netto 1992)
3. **Acherontiella** Absolon, 1913 (18 spp.) (see Barra 1994; Thibaud 1990)
4. **Acheroxenylla** Ellis, 1976 (3 spp.) (see Fjellberg 1991e)
5. **Barbagastrura** Massoud *et al.*, 1975 (1 sp.)
6. **Biscoia** Salmon, 1962 (1 sp.)
7. **Bonetogastrura** Thibaud, 1975 (8 spp.) (see Hermosilla *et al.* 1985; Thibaud 1980b)
8. **Ceratophysella** Börner, 1932 (102 spp.) (see Deharveng and Bourgeois 1991; Jordana and Arbea 1990b)
9. **Chinogastrura** Rusek, 1967 (1 sp.)
10. **Choreutinula** Paclt, 1944 (6 spp.) (see Gers and Deharveng 1985)
11. **Cosberella** Wray, 1963 (1 sp.)
12. **Denigastrura** Stach, 1949 (1 sp.)
13. **Franzura** Cassagnau and Deharveng 1976 (1 sp.)
14. **Gnathogastrura** Diaz and Najt, 1983 (1 sp.)
15. **Gomphiocephalus** Carpenter, 1908 (1 sp.)
16. **Hypogastrura** Bourlet, 1839 (136 spp.) (see Babenko and Thibaud 1990; Christiansen and Bellinger 1992; Hart and Waltz 1995; Jordana and Arbea 1990b; Lee and Kim 1995b; Najt *et al.* 1984)

17. **Jacutogastrura** Martynova, 1981 (1 sp.)
18. **Knowltonella** Wray, 1958 (1 sp.) (see Fjellberg 1991b)
19. **Mesachorutes** Absolon, 1900 (4 spp.)
20. **Mesogastrura** Bonet, 1930 (5 spp.)
21. **Microgastrura** Stach, 1922 (5 spp.) (see Deharveng and Najt 1989; Simon-Benito and Pozo-Martinez 1984)
22. **Mitchellania** Wray, 1953 (15 spp.)
23. **Mucrella** Fjellberg, 1985b (5 spp.) (see Fjellberg 1987b, 1992a)
24. **Neobeckerella** Wray, 1952 (1 sp.)
25. **Octoacanthella** Martynova, 1961 (1 sp.) (see Deharveng and Diaz 1984)
26. **Ongulogastrura** Thibaud and Massoud, 1983a (1 sp.)
27. **Orogastrura** Deharveng and Gers, 1979 (7 spp.) (see Arbea and Jordana 1990c)
28. **Parawillemia** Izarra, 1975 (1 sp.)
29. **Pseudacherontides** Djanaschvili, 1971 (9 spp.)
30. **Schaefferia** Absolon, 1900 (23 spp.) (see Deharveng and Thibaud 1980; Kniss 1985; Thibaud 1972, 1995b; Yoshii 1991)
31. **Schoettella** Schäffer, 1896 (8 spp.) (see Diaz and Palacios-Vargas 1983)
32. **Stenogastrura** Christiansen and Bellinger, 1980 (1 sp.)
33. **Tafallia** Bonet, 1947 (2 spp.)
34. **Triacanthella** Schäffer, 1897 (21 spp.) (see Cassagnau and Deharveng 1974; Dunger and Zivadinovic 1983)
35. **Typhlogastrura** Bonet, 1930 (12 spp.) (see Hermosilla *et al.* 1985; Thibaud 1980b)
36. **Willemgastrura** Oliveira and Thibaud, 1988 (1 sp.)
37. **Willemia** Börner, 1901 (29 spp.) (see Fjellberg 1991d; Gers and Deharveng 1985; Thibaud 1994b; Thibaud and Lee 1994; Weiner 1991b)
38. **Xenylla** Tullberg, 1869 (125 spp.) (see André 1988a,b; Culik and Deharveng 1986; Deharveng and Najt 1989; Fjellberg 1991e; Gama 1964, 1987, 1988a,b; Gama and Oliveira 1994; Jordana 1993; Najt and Weiner 1991; Najt *et al.* 1990; Weiner and Najt 1991b)
39. **Xenyllogastrura** Denis, 1932 (7 spp.) (see Fjellberg 1991e; Jordana and Arbea 1992)

1.1.2.3 Subfamily ISOTOGASTRURINAE (2 spp.)

1. **Isotogastrura** Thibaud and Najt, 1992 (2 spp.) (see Fjellberg 1995b)

1.1.3 Family NEANURIDAE

1.1.3.1 Subfamily CAPUTANURININAE (7 spp.)

1. **Caputanurina** Lee, 1983 (5 spp.) (see Najt and Weiner 1992)
2. **Leenurina** Najt and Weiner, 1992 (2 spp.)

1.1.3.2 Subfamily FRIESEINAE (148 spp.)

1. **Friesea** Dalla Torre, 1895 (147 spp.) (see Arbea and Jordana 1991b, 1993; Christiansen and Bellinger 1992; Deharveng and Bedos 1991; Jordana *et al.*

1990; Palacios-Vargas 1988; Palacios-Vargas and Acosta 1994; Thibaud 1993a, 1995a)

2. **Gisinea** Massoud, 1965 (1 sp.)

1.1.3.3 *Subfamily MORULININAE (17 spp.)*

1. **Morulina** Börner, 1906 (17sp.) (see Deharveng and Weiner 1984; Tanaka 1984)

1.1.3.4 *Subfamily NEANURINAE (606 spp.)*

1. **Adbiloba** Stach, 1951 (6 spp.) (see Cassagnau 1993c)
2. **Afrobella** Cassagnau, 1983 (3 spp.)
3. **Albanura** Cassagnau and Peja, 1979 (1 sp.) (see Deharveng 1982e)
4. **Americanura** Cassagnau and Palacios-Vargas, 1983 (13 spp.) (see Christiansen and Reddel 1986; Palacios-Vargas and Najt 1986)
5. **Australonura** Cassagnau 1980 (17sp.) (see Deharveng and Greenslade 1990; Deharveng and Wise 1987; Greenslade and Deharveng 1990)
6. **Balkanura** Cassagnau, 1979 (2 spp.)
7. **Bilobella** Caroli, 1912 (12 spp.) (see Cassagnau *et al.* 1985; Deharveng 1981b, 1984b)
8. **Blasconura** Cassagnau, 1983 (9 spp.) (see Cassagnau 1988; Palacios-Vargas and Diaz 1992)
9. **Blasconurella** Deharveng and Bedos, 1992 (5 spp.)
10. **Caledonura** Deharveng, 1988a (1 sp.)
11. **Calvinura** Cassagnau, 1988 (2 spp.)
12. **Camerounura** Cassagnau, 1991a (1 sp.)
13. **Cansilianura** Dallai and Fanciulli, 1983 (1 sp.) (see Fanciulli *et al.* 1991b)
14. **Catalanura** Deharveng, 1982 (3 spp.) (see Arbea and Jordana 1991a)
15. **Caucasanura** Kuznetsova and Potapov, 1988 (2 spp.) (see Deharveng 1989c)
16. **Chaetobella** Cassagnau, 1983 (9 spp.) (see Cassagnau 1993c)
17. **Chiolavia** Deharveng, 1991 (2 spp.)
18. **Christobella** Fjellberg, 1985b (1 sp.)
19. **Coecoloba** Yosii, 1956 (9 spp.) (see Deharveng 1983b)
20. **Coreanura** Deharveng and Weiner, 1984 (1 sp.)
21. **Crossodonthina** Yosii, 1954 (7 spp.) (see Lee and Kim 1990)
22. **Cryptonura** Cassagnau, 1979 (4 spp.)
23. **Deuterobella** Yoshii and Suhardjono, 1992a (3 spp.)
24. **Deutonura** Cassagnau, 1979 (55 spp.) (see Arbea and Jordana 1991a; Deharveng 1982d, 1984b, 1986b,e, 1987e, 1989e; Traser *et al.* 1993)
25. **Digitanura** Deharveng, 1987d (1 sp.)
26. **Echinanura** Carpenter, 1934 (2 spp.)
27. **Ectonura** Cassagnau, 1980 (3 spp.) (see Barra 1994; Deharveng 1988a)
28. **Elgonura** Cassagnau, 1984 (1 sp.)
29. **Endonura** Cassagnau, 1979 (26 spp.) (see Dallai 1983; Fjellberg 1985b)
30. **Girkanura** Kuznetsova and Potapov, 1988 (1 sp.)

31. **Gnatholonche** Börner, 1906 (25sp.) (see Cassagnau 1993*b*)
32. **Hazaranura** Cassagnau, 1991*c* (1 sp.)
33. **Hemilobella** Deharveng and Greenslade, 1992 (4 spp.)
34. **Himalmeria** Cassagnau, 1984 (3 spp.) (see Cassagnau 1993*b*)
35. **Hyperlobella** Cassagnau, 1988 (1 sp.)
36. **Imparitubercula** Stach, 1951 (1 sp.)
37. **Inameria** Cassagnau, 1983 (2 spp.) (see Cassagnau 1984)
38. **Lathriopyga** Caroli, 1910 (8 spp.) (see Barra 1993; Deharveng 1985)
39. **Lobella** Börner, 1906 (17 spp.) (see Cassagnau and Deharveng 1984; Deharveng and Weiner 1984; Lee and Kim 1990)
40. **Lobellina** Yosii, 1956 (21 spp.) (see Deharveng and Weiner 1984)
41. **Metanura** Yosii, 1954 (4 spp.) (see Deharveng and Weiner 1984)
42. **Monobella** Cassagnau, 1979 (9 spp.) (see Deharveng 1984*b*, 1986*a*)
43. **Morulodes** Cassagnau, 1955 (3 spp.) (see Christiansen and Bellinger 1980)
44. **Nahuanura** Palacios-Vargas and Najt, 1986 (1 sp.)
45. **Neanura** MacGillivray, 1893 (39 spp.) (see Deharveng 1979*c*; Lee and Kim 1990; Li 1992)
46. **Neanurella** Cassagnau, 1971 (3 spp.) (see Weiner 1973)
47. **Nepalanura** Yosii, 1966 (1 sp.) (see Cassagnau 1991*c*)
48. **Nepalimeria** Cassagnau, 1984 (6 spp.) (see Cassagnau 1993*a*)
49. **Nilgirella** Cassagnau, 1983 (5 spp.) (see Cassagnau 1983*a*)
50. **Paleonura** Cassagnau, 1982 (41sp.) (see Cassagnau 1991*c*; Cassagnau and Oliveira 1990; Deharveng and Bedos 1993*b*; Deharveng and Greenslade 1992; Palacios-Vargas and Diaz 1992; Palacios-Vargas and Gómez-Anaya 1995; Thibaud and Najt 1993)
51. **Palmanura** Cassagnau and Palacios-Vargas, 1983 (3 spp.) (see Palacios-Vargas 1984, 1986)
52. **Paralobella** Cassagnau and Deharveng, 1984 (1 sp.)
53. **Paramanura** Cassagnau, 1986*a* (2 spp.) (see Cassagnau 1991*c*; Cassagnau and Oliveira 1990)
54. **Paranura** Axelson, 1902 (32 spp.) (see Cassagnau 1991*c*; Deharveng 1989*b*; Palacios-Vargas and Deharveng 1987)
55. **Parectonura** Deharveng, 1988*a* (1 sp.)
56. **Parvatinura** Cassagnau, 1982 (4 spp.) (see Cassagnau 1993*b*)
57. **Pectinura** Cassagnau, 1983 (1 sp.)
58. **Penelopella** Cassagnau, 1986*a* (1 sp.)
59. **Phradmon** Greenslade and Deharveng, 1991 (6 spp.)
60. **Phyllimeria** Delamare Deboutteville, 1948 (4 spp.) (see Cassagnau 1984)
61. **Pronura** Delamare Deboutteville, 1953 (27sp.) (see Cassagnau 1991*c*; Cassagnau and Oliveira 1990; Deharveng and Bedos 1993*b*; Greenslade and Deharveng 1991)
62. **Propeanura** Yosii, 1956 (18 spp.) (see Deharveng and Weiner 1984)
63. **Protanura** Börner, 1906 (11 spp.) (see Christiansen and Bellinger 1992; Thibaud and Massoud 1980)
64. **Protolobella** Cassagnau, 1983 (1 sp.)

65. **Pseudadbiloba** Massoud, 1963 (1 sp.)
66. **Pseudobiloba** Stach, 1951 (1 sp.)
67. **Pumilinura** Cassagnau, 1979 (5 spp.) (see Barra 1993)
68. **Rambutanura** Deharveng 1988b (3 spp.)
69. **Riozura** Cassagnau, 1983 (1 sp.)
70. **Sensillanura** Deharveng, 1981 (6 spp.)
71. **Siamanura** Deharveng, 1987b (14 spp.) (see Suhardjono and Deharveng 1992)
72. **Singalimeria** Cassagnau, 1984 (1 sp.) (see Cassagnau 1990b)
73. **Sphaeronura** Cassagnau, 1983 (1 sp.)
74. **Stenomeria** Cassagnau, 1990b (1 sp.)
75. **Synameria** Cassagnau, 1983 (3 spp.) (see Cassagnau 1990b)
76. **Tamulmeria** Cassagnau, 1988 (2 spp.)
77. **Telobella** Cassagnau, 1983 (1 sp.)
78. **Tetraloba** Lee, 1983 (1 sp.)
79. **Thaianura** Yosii, 1961 (1 sp.)
80. **Thaumanura** Börner, 1932 (5 spp.)
81. **Travura** Cassagnau and Deharveng, 1980 (3 spp.) (see Cassagnau 1993c)
82. **Vitronura** Yosii, 1969 (18 spp.) (see Cassagnau and Deharveng 1981; Lee and Kim 1990)
83. **Womersleya** Denis, 1948 (3 spp.) (see Lee and Kim 1990)
84. **Yetimeria** Cassagnau, 1984 (18 spp.)
85. **Yuukianura** Yosii, 1955 (3 spp.) (see Deharveng and Greenslade 1992)
86. **Zelandanura** Deharveng and Wise, 1987 (1 sp.)
87. **Zealandmeria** Stach, 1949 (3 spp.)

1.1.3.5 Subfamily PSEUDACHORUTINAE (367 spp.)

1. **Aethiopella** Handschin, 1942 (20 spp.) (see Christiansen and Bellinger 1992)
2. **Aethiopellina** Delamare Deboutteville, 1951 (4 spp.) (see Najt *et al.* 1990)
3. **Anurachorutes** Kuznetsova and Potapov, 1988 (1 sp.)
4. **Anurida** Laboulbène, 1865 (68 spp.) (see Najt *et al.* 1991; Pomorski 1994a; Pomorski and Skarzynski 1994)
5. **Anuridella** Willem, 1906 (3 spp.)
6. **Anuritelsa** Womersley, 1939 (1 sp.)
7. **Arlesia** Handschin, 1942 (6 spp.) (see Thibaud and Massoud 1983b)
8. **Arlesiella** Delamare Deboutteville, 1951 (6 spp.)
9. **Brasilimeria** Stach, 1949 (2 spp.)
10. **Cassagnaudina** Massoud, 1967 (4 spp.)
11. **Cassagnaurida** Salmon, 1964 (1 sp.)
12. **Cephalachorutes** Bedos and Deharveng, 1991 (11 spp.)
13. **Ceratrimeria** Börner, 1906 (11 spp.) (see Najt and Weiner 1991)
14. **Chihuahuachorutes** Palacios-Vargas, 1990a (1 sp.)
15. **Delamarellina** Rapoport and Rubio, 1963 (3 spp.)
16. **Furculanurida** Massoud, 1967 (10 spp.) (see Najt *et al.* 1990)

17. **Gamachorutes** Cassagnau, 1978 (1 sp.)
18. **Gastranurida** Bagnall, 1949 (1 sp.)
19. **Grananurida** Yosii, 1954 (3 spp.) (see Rusek 1991*b*; Weiner and Najt 1985*b*)
20. **Halachorutes** Arlé, 1967 (1 sp.)
21. **Hylaeonura** Arlé, 1966 (1 sp.)
22. **Intermediurida** Najt *et al.*, 1990 (1 sp.)
23. **Kenyura** Salmon, 1954 (5 spp.)
24. **Koreanurina** Najt and Weiner, 1992 (2 spp.)
25. **Lanzhotia** Rusek, 1985*c* (1 sp.)
26. **Linnaniemia** Philpitschenko, 1926 (2 spp.)
27. **Meganurida** Carpenter, 1934 (1 sp.)
28. **Micranurida** Börner, 1901 (22 spp.) (see Christiansen and Bellinger 1992; Deharveng 1982*g*)
29. **Neotropiella** Handschin, 1942 (12 spp.) (see Diaz and Najt 1994; Najt *et al.* 1990)
30. **Notachorudina** Cassagnau and Rapoport, 1962 (1 sp.)
31. **Oudemansia** Schött, 1893 (8 spp.) (see Christiansen and Bellinger 1992)
32. **Paranurida** Skarzynski and Pomorski, 1994 (1 sp.)
33. **Philotella** Najt and Weiner, 1985 (4 spp.) (see Kniss and Thibaud 1995)
34. **Platanurida** Carpenter, 1925 (3 spp.)
35. **Pratanurida** Rusek, 1973 (8 spp.) (see Arbea and Jordana 1990*b*)
36. **Protachorutes** Cassagnau, 1955 (2 spp.)
37. **Pseudachorudina** Stach, 1949 (19 spp.) (see Jordana and Arbea 1989*b*; Simon-Benito and Pozo-Martinez 1988)
38. **Pseudachorutella** Stach, 1949 (9 spp.) (see Najt *et al.* 1990; Weiner and Najt 1991*b*)
39. **Pseudachorutes** Tullberg, 1871 (85 spp.) (see Arbea and Jordana 1989*a*, 1991*b*; Barra 1993; Diaz and Najt 1994; Najt and Weiner 1991; Najt *et al.* 1990, 1991; Oliveira and Deharveng 1994; Palacios-Vargas 1990*a*; Simon-Benito and Pozo-Martinez 1988; Snider 1981*a*; Weiner and Najt 1991*b*)
40. **Pseudanurida** Schött, 1901 (5 spp.) (see Lee and Kim 1994; Murphy 1971)
41. **Quatacanthella** Salmon, 1945 (1 sp.)
42. **Rusekella** Deharveng, 1983 (7 spp.) (see Deharveng 1982*g*; Arbea and Jordana 1991*a*)
43. **Stachorutes** Dallai, 1973 (7 spp.) (see Arbea and Jordana 1991*b*; Barra 1994; Deharveng and Lienhard 1983)
44. **Tremoisea** Cassagnau, 1973 (2 spp.)

1.1.3.6 Subfamily UCHIDANURINAE (15 spp.)

1. **Acanthanura** Börner, 1906 (1 sp.)
2. **Assamanura** Cassagnau, 1980 (1 sp.)
3. **Caledonimeria** Delamare Deboutteville and Massoud, 1963 (1 sp.) (see Vannier and Najt 1991)

4. **Denisimeria** Massoud, 1965 (3 spp.)
5. **Holacanthella** Börner, 1906 (5 spp.)
6. **Megalanura** Ellis and Bellinger, 1973 (1 sp.)
7. **Uchidanura** Yosii, 1954 (2 spp.) (see Cassagnau 1980*b*; Greenslade 1991*b*; Mari Mutt 1979*b*)
8. **Womersleymeria** Stach, 1949 (1 sp.)

1.1.4 Family ODONTELLIDAE (100 spp.)

1. **Afrodontella** Deharveng, 1981 (1 sp.)
2. **Austrodontella** Ellis and Bellinger, 1973 (2 spp.)
3. **Axenyllodes** Stach, 1949 (10 spp.) (see Fjellberg 1988*b*, 1995*a*; Thibaud 1995*a*; Vasquez and Palacios-Vargas 1989)
4. **Caufrenyllodes** Greenslade and Deharveng, 1984 (1 sp.)
5. **Odontella** Schäffer, 1897 (22 spp.) (see Arbea and Lucianez 1991; Bedos and Deharveng 1990; Rusek 1991*c*; Weiner and Najt 1991*b*)
6. **Odontellina** Deharveng, 1981 (3 spp.) (see Thibaud and Christian 1989)
7. **Odontellodes** Stach, 1949 (1 sp.)
8. **Pseudostachia** Arlé, 1968 (4 spp.) (see Palacios-Vargas and Najt 1985; Fjellberg 1995*a*)
9. **Pseudoxenyllodes** Kuznetsova and Potapov, 1988 (1 sp.)
10. **Stachia** Folsom, 1932 (1 sp.)
11. **Stachiomella** Wray, 1957 (1 sp.)
12. **Superodontella** Stach, 1949 (48 spp.) (see Arbea 1988*a,b*; Arbea and Jordana 1991*b*; Arbea and Weiner 1991; Bedos and Deharveng 1990; Díaz and Najt 1994; Rusek 1991*c*)
13. **Xenyllodes** Axelson, 1903 (5 spp.) (see Fjellberg 1985*d*)

1.1.5 Family ONYCHIURIDAE

1.1.5.1 Subfamily ONYCHIURINAE (427 spp.) (see Weiner 1996)

1. **Archaphorura** Bagnall, 1949 (32 spp.) (see Christian 1986*d*, 1993*a*; Fjellberg 1987*a*; Kaprus and Weiner 1994; Simon and Lucianez 1994)
2. **Hymenaphorura** Bagnall, 1948 (35 spp.) (see Arbea and Jordana 1994; Pomorski 1990*b*, 1992*a*; Pomorski and Weichsel 1993; Weiner and Fjellberg 1994)
3. **Kalaphorura** Absolon, 1901 (7 spp.)
4. **Ongulonychiurus** Thibaud and Massoud, 1986*b* (1 sp.)
5. **Onychiurus** Gervais, 1841 (137 spp.) (see Arbea and Jordana 1994; Beruete *et al.* 1994; Deharveng and Gouze 1984; Hale 1980; Khanislamova 1986; Lee and Kim 1994, 1995*b*; Lin and Xia 1985; Oliveira and Thibaud 1992; Pomorski 1990*a*; Simon and Lucianez 1994; Skarzynski 1991; Thibaud 1993*a*; Thibaud and Lee 1994; Weiner 1986*a*; Weiner and Najt 1991*b*)
6. **Paronychiurus** Bagnall, 1948 (68 spp.) (see Lee and Park 1986; Weiner 1989*b*)
7. **Probolaphorura** Dunger, 1977 (3 spp.) (see Dunger 1976*a*)

8. **Protaphorura** Absolon, 1901 (143 spp.) (see Arbea and Jordana 1994; Arbea *et al.* 1986; Kaprus and Weiner 1994; Najt *et al.* 1991; Palissa 1986; Pomorski 1990c, 1993, 1994b; Simon and Lucianez 1994; Thibaud and Lee 1994; Thibaud and Peja 1994; Weiner 1990; Weiner and Stomp 1995)
9. **Uralaphorura** Martynova, 1978 (1 sp.)

1.1.5.2 Subfamily PACHYTULLBERGIINAE (3 spp.)

1. **Pachytullbergia** Bonet, 1947 (1 sp.)
2. **Paleotullbergia** Delamare Deboutteville, 1951 (1 sp.)
3. **Sensiphorura** Rusek, 1976 (1 sp.)

1.1.5.3 Subfamily TETRODONTOPHORINAE (4 spp.)

1. **Homaloproctus** Börner, 1909 (1 sp.)
2. **Lophognathella** Börner, 1908 (1 sp.)
3. **Tetrodontophora** Reuter, 1892 (1 sp.) (see Dallai 1973b; Fanciulli *et al.* 1991a)
4. **Ussuriaphorura** Martynova, 1979 (1 sp.)

1.1.5.4 Subfamily TULLBERGIINAE (168 spp.) (see Zimdars and Dunger 1994)

1. **Anaphorura** Izarra, 1972 (1 sp.)
2. **Boudinotia** Weiner and Najt, 1991a (1 sp.)
3. **Chaetophorura** Rusek, 1976 (12 spp.) (see Christiansen and Bellinger 1992; Fjellberg 1988b)
4. **Clavaphorura** Salmon, 1943 (1 sp.)
5. **Dinaphorura** Bagnall, 1935 (13 spp.) (see Weiner and Najt 1991a)
6. **Doutnacia** Rusek, 1974 (2 spp.) (see Massoud and Thibaud 1985)
7. **Fissuraphorura** Rusek, 1991e (5 spp.) (see Lucianez and Simon 1992b)
8. **Granuliphorura** Rusek, 1976 (1 sp.)
9. **Jevania** Rusek, 1978 (2 spp.)
10. **Karlstejnina** Rusek, 1974 (5 spp.) (see Fjellberg 1974a; Weiner 1983)
11. **Marcuzziella** Rusek, 1975 (1 sp.)
12. **Mesaphorura** Börner, 1901 (49 spp.) (see Arbea and Jordana 1991b; Arbea and Selga 1994; Greenslade 1992b; Jordana 1993; Jordana and Arbea 1994; Najt *et al.* 1990; Oliveira and Thibaud 1992; Rusek 1982a; Simon *et al.* 1994; Weiner 1991a; Weiner and Thibaud 1991)
13. **Metaphorura** Bagnall, 1936 (6 spp.)
14. **Multivesicula** Rusek, 1982b (6 spp.) (see Rusek 1991a)
15. **Najtiaphorura** Weiner and Thibaud, 1991 (2 spp.)
16. **Neonaphorura** Bagnall, 1935 (8 spp.) (see Arbea 1991; Arbea and Mateos 1991; Weiner and Thibaud 1991)
17. **Neotullbergia** Bagnall, 1935 (6 spp.)
18. **Paratullbergia** Womersley, 1930 (8 spp.) (see Lucianez *et al.* 1991)
19. **Pongeella** Rusek, 1991a (2 spp.)
20. **Prabhergia** Salmon, 1965 (2 spp.) (see Yoshii and Suhardjono 1989)

21. **Psammophorura** Thibaud and Weiner 1994 (1 sp.)
22. **Rotundiphorura** Rusek, 1991e (1 sp.)
23. **Scaphaphorura** Petersen, 1965 (3 spp.) (see Simon and Lucianez 1990b; Thibaud 1994b)
24. **Stenaphorura** Absolon, 1900 (2 spp.)
25. **Tillieria** Weiner and Najt, 1991a (2 spp.) (see Weiner and Najt 1994)
26. **Tullbergia** Lubbock, 1876 (19 spp.) (see Dunger 1991b)
27. **Tullbergiella** Izarra 1965 (2 spp.)
28. **Wankeliella** Rusek, 1975 (4 spp.) (see Simon and Jordana 1994)
29. **Weinera** Thibaud, 1993a (1 sp.)

1.1.6 Family *PODURIDAE* (1 sp.)

1. **Podura** Linnaeus, 1758 (1 sp.)

1.2 Superfamily *Entomobryoidea* (= *Entomobryomorpha*)

1.2.1 Family *ACTALETIDAE* (9 spp.)

1. **Actaletes** Giard, 1889 (1 sp.) (see Dallai and Malatesta 1973; Delamare Deboutteville 1964)
2. **Spinactaletes** Soto-Adames, 1988b (8 spp.) (see also Soto-Adames 1987)

1.2.2 Family *COENALETIDAE* (2 spp.)

1. **Coenaletes** Bellinger, 1985a (2 spp.)

1.2.3 Family *CYPHODERIDAE* (123 spp.)

1. **Calobatinus** Silvestri, 1918 (4 spp.)
2. **Cephalophilus** Delamare Deboutteville, 1948 (3 spp.)
3. **Cyphoda** Delamare Deboutteville 1948 (9 spp.) (see Yoshii 1987)
4. **Cyphoderinus** Denis, 1942 (1 sp.)
5. **Cyphoderodes** Silvestri, 1910 (7 spp.) (see Yoshii 1992a)
6. **Cyphoderus** Nicolet, 1842 (60 spp.) (see Gama 1988c; Thibaud and Najt 1987; Yoshii 1987)
7. **Delamarerus** Mitra, 1977 (2 spp.)
8. **Megacyphoderus** Delamare Deboutteville, 1948 (7 spp.)
9. **Mimoderus** Yosii, 1980 (3 spp.)
10. **Paracyphoderus** Delamare Deboutteville, 1948 (1 sp.)
11. **Pseudocyphoderus** Imms, 1912 (1 sp.) (see Mari Mutt 1977)
12. **Serroderus** Delamare Deboutteville, 1948 (20 spp.) (see Yoshii 1987, 1992b)
13. **Setoderus** Yosii, 1959 (5 spp.)

1.2.4 Family ENTOMOBRYIDAE

1.2.4.1 Subfamily ENTOMOBRYINAE (1130 spp.)

1. **Acanthocyrtus** Handschin, 1925 (7 spp.)
2. **Acanthurella** Börner, 1906 (7 spp.)
3. **Americabrya** Mari Mutt and Palacios-Vargas, 1987 (3 spp.)
4. **Botryanura** Chelnokov, 1987 (1 sp.)
5. **Calx** Christiansen, 1958 (3 spp.)
6. **Coecobrya** Yosii, 1956 (20 spp.) (see Christiansen and Bellinger 1992; Deharveng 1990; Greenslade 1992a)
7. **Ctenocyrtinus** Arlé, 1959 (3 spp.)
8. **Desertia** Chelnokov, 1979 (1 sp.)
9. **Deuterosinella** Salmon, 1943 (1 sp.)
10. **Drepanosira** Bonet, 1942 (15 spp.)
11. **Drepanura** Schött, 1891 (29 spp.) (see Kaprus and Szeptycki 1992)
12. **Entomobrya** Rondani, 1861 (217 spp.) (see Christiansen and Bellinger 1992; Diaz and Najt 1994; Lee and Park 1992; South 1961)
13. **Entomobryoides** Maynard, 1951 (10 spp.) (see Christiansen and Bellinger 1992)
14. **Epimetrura** Schött, 1925 (3 spp.) (see Greenslade and Sutrisno 1994)
15. **Hawinella** Bellinger and Christiansen, 1974 (2 spp.) (see Christiansen and Bellinger 1992)
16. **Himalanura** Baijal, 1958 (14 spp.)
17. **Homidia** Börner, 1906 (31 spp.) (see Christiansen and Bellinger 1992; Lee and Lee 1981)
18. **Isotobrya** Womersley, 1934 (2 spp.)
19. **Janetschekbrya** Yosii, 1971 (3 spp.) (see Loring 1984; Mari Mutt and Palacios-Vargas 1987; Snider 1981c)
20. **Lepidiaphanus** Salmon, 1949 (2 spp.)
21. **Lepidobrya** Womersley, 1937 (4 spp.)
22. **Lepidocyrtoides** Schött 1917 (15 spp.) (see Yoshii and Greenslade 1994)
23. **Lepidocyrtus** Bourlet, 1839 (185 spp.) (see Arbea and Jordana 1990d; Christiansen and Bellinger 1991; Hüther 1986; Mari Mutt 1986; Rusek 1985d; Szeptycki 1967a; Traser and Christian 1992; Yoshii and Greenslade 1994)
24. **Lepidokrugeria** Coates, 1969 (1 sp.)
25. **Lepidoregia** Delamare Deboutteville, 1948 (1 sp.)
26. **Lepidosinella** Handschin, 1920 (1 sp.)
27. **Lepidosira** Schött, 1925 (36 spp.) (see Greenslade 1994a)
28. **Marginobrya** Yoshii, 1992a (1 sp.)
29. **Mesentotoma** Salmon, 1942 (6 spp.) (see Christiansen and Bellinger 1992)
30. **Metasinella** Denis, 1929 (1 sp.) (see Mari Mutt and Gruia 1983)
31. **Nothobrya** Arlé, 1961 (1 sp.)
32. **Prodrepanura** Stach, 1963 (1 sp.)
33. **Pseudocyrtus** Salmon, 1956 (3 spp.)

34. **Pseudosinella** Schäffer, 1897 (247 spp.) (see Arbea and Jordana 1990*d*; Ardanaz and Jordana 1985; Christiansen 1982*b*; Christiansen and Luther 1986; Christiansen *et al.* 1983, 1990; Deharveng 1988*c*; Deharveng and Gouze 1986; Gama 1984*a*, 1988*d*; Gouze and Deharveng 1987; Lucianez and Simon 1994*b*; Mari Mutt 1986; Mateos 1993; Rusek 1985*d*; Stomp 1971, 1986; Stomp *et al.* 1991)
35. **Seira** Lubbock, 1869 (168 spp.) (see Christiansen and Bellinger 1992; Jordana and Arbea 1989*a*; Mari Mutt 1987*a, b*; Tosi and Parisi 1990)
36. **Setogaster** Salmon, 1951 (6 spp.)
37. **Sinella** Brook, 1882 (42 spp.) (see Chen and Christiansen 1993; Greenslade 1992*a*)
38. **Sinelloides** Bonet, 1942 (2 spp.)
39. **Sulcuncus** Mills, 1938 (9 spp.) (see Mari Mutt and Gruia 1983)
40. **Urewera** Salmon, 1938 (15 spp.)
41. **Willowsia** Shoebottom, 1917 (19 spp.) (see Christiansen and Bellinger 1992; Mari Mutt 1981*d*)

1.2.4.2 Subfamily ORCHESELLINAE (235 spp.)

1. **Alloscopus**, Börner, 1906 (7 spp.) (see Mari Mutt 1982; Yoshii and Suhardjono 1992*a*)
2. **Australotomurus** Stach, 1947 (6 spp.) (see Mari Mutt and Greenslade 1985)
3. **Bessoniella** Deharveng and Thibaud, 1989*b* (1 sp.)
4. **Corynothrix** Tullberg, 1876 (1 sp.) (see Mari Mutt 1984*a*)
5. **Dicranocentrus** Schött, 1893 (63 spp.) (see Mari Mutt 1979*a*, 1981*a,b,c*, 1983*a*, 1985*d*, 1988; Najt *et al.* 1988; Yoshii and Suhardjono 1989)
6. **Dicranorchesella** Mari Mutt, 1977 (3 spp.)
7. **Heteromurtrella** Mari Mutt, 1979 (18 spp.) (see Najt *et al.* 1988)
8. **Heteromurus** Wankel, 1860 (11 spp.) (see Mari Mutt 1983*a*, 1985*a,c*, 1987*c*; Nosek and Paoletti 1985)
9. **Mastigoceras** Handschin, 1924 (1 sp.) (see Cassagnau and Oliveira 1992; Mari Mutt 1978*c*)
10. **Neorchesella** Mari Mutt, 1981 (2 spp.)
11. **Orchesella** Templeton, 1835 (105 spp.) (see Frati and Szeptycki 1990; Frati *et al.* 1992*a,b*; Mari Mutt 1985*b*)
12. **Orchesellides** Bonet, 1930 (8 spp.) (see Mari Mutt 1983*c*)
13. **Pseudodicranocentrus** Mari Mutt, 1981 (3 spp.)
14. **Verhoeffiella** Absolon, 1900 (6 spp.) (see Nosek and Paoletti 1985)

1.2.5 Family ISOTOMIDAE (1028 spp.)

1. **Aackia** Yosii, 1966 (1 sp.)
2. **Acanthomurus** Womersley, 1934 (8 spp.) (see Greenslade 1989)
3. **Agrenia** Börner, 1906 (8 spp.) (see Fjellberg 1986*c*, 1988*d*)
4. **Antarcticinella** Salmon, 1965 (1 sp.)

5. **Antarctophorus** Potapov, 1991a (1 sp.)
6. **Anurophorouzelia** Stach, 1947 (1 sp.)
7. **Anurophorus** Nicolet, 1842 (40 spp.) (see Christiansen and Bellinger 1992; Dunger 1982; Fjellberg 1974b; Lawrence 1978b; Potapov 1989)
8. **Appendisotoma** Stach, 1947 (18 spp.) (see Christian 1986a; Traser *et al.* 1993)
9. **Araucanocyrtus** Massoud and Rapoport, 1968 (1 sp.) (see Greenslade 1989)
10. **Archisotoma** Linnaniemi, 1912 (14 spp.) (see Fjellberg 1980b; Fjellberg and Poinot 1975; Thibaud 1993a)
11. **Arlea** Womersley, 1939 (3 spp.) (see Mendonca and Arle 1987)
12. **Astephanus** Denis, 1926 (1 sp.) (see Suhardjono and Greenslade 1994)
13. **Axelsonia** Börner, 1906 (7 spp.)
14. **Ballistura** Börner, 1906 (18 spp.) (see Lucianez and Simon 1994a)
15. **Blissia** Rusek, 1985b (1 sp.)
16. **Boernerella** Denis, 1925 (2 spp.)
17. **Bonetrura** Christiansen and Bellinger, 1980 (1 sp.)
18. **Cheirutoma** Bagnall, 1949 (1 sp.)
19. **Clavisotoma** Ellis, 1970 (20 spp.)
20. **Cliforga** Wray, 1952 (1 sp.)
21. **Coloburella** Latzel, 1918 (3 spp.)
22. **Cryptopygus** Willem, 1901 (71 spp.) (see Bernard and Snider 1994; Diaz and Najt 1994; Lawrence 1978b,c; Palacios-Vargas 1992a; Schaller and Kopeszki 1991)
23. **Dagamaea** Yosii, 1965 (2 spp.)
24. **Desoria** Nicolet, 1841 (92 spp.) (see Christiansen and Bellinger 1992; Fjellberg 1978b; Gers and Najt 1983; Waltz and Hart 1995a,c)
25. **Dimorphotoma** Grinbergs, 1975 (2 spp.)
26. **Folsomia** Willem, 1902 (103 spp.) (see Bödvarsson 1970a; Deharveng 1982b; Dunger 1991c; Dunger and Zivadinovic 1989; Grow and Christiansen 1976; Hermosilla *et al.* 1984a; Kseneman 1936; Lawrence 1973b; Lee and Kim 1994; Najt 1980; Rusek 1980a; Wetton 1987; Zhao and Tamura 1992)
27. **Folsomides** Stach, 1922 (49sp.) (see Fjellberg 1992b; Gers and Deharveng 1985; Lucianez and Simon 1991; Poinot-Balaguer and Barra 1982; Simon and Lucianez 1990a; Suhardjono and Greenslade 1994)
28. **Folsomina** Denis, 1931 (3 spp.) (see Zhao and Tamura 1992)
29. **Folsomotoma** Bagnall, 1949 (8 spp.) (see Greenslade 1986a, 1989)
30. **Gnathisotoma** Cassagnau, 1958 (6 spp.) (see Yoshii 1990)
31. **Gnathofolsomia** Deharveng and Christian, 1984 (1 sp.)
32. **Gressittacantha** Wise, 1967 (1 sp.) (see Dallai *et al.* 1988; Lawrence 1978b)
33. **Halisotoma** Bagnall, 1949 (8 spp.) (see Christiansen and Bellinger 1992)
34. **Haploisotoma** Izarra, 1965 (1 sp.)
35. **Heteroisotoma** Stach, 1947 (4 spp.) (see Potapov and Stebaeva 1992)

36. **Hydroisotoma** Stach, 1947 (1 sp.)
37. **Isotoma** Bourlet, 1839 (53 spp.) (see Fjellberg 1979; Lee *et al.* 1993; Rusek 1984b)
38. **Isotomedia** Salmon, 1944 (1 sp.)
39. **Isotomiella** Bagnall, 1939 (22 spp.) (see Bedos and Deharveng 1994; Christiansen and Bellinger 1992; Deharveng 1989a; Deharveng and Fjellberg 1993; Deharveng and Oliveira 1990; Deharveng and Suhardjono 1994; Oliveira and Deharveng 1990)
40. **Isotominella** Delamare Deboutteville, 1948 (2 spp.)
41. **Isotomodella** Martynova, 1968 (1 sp.) (see Fjellberg 1975b)
42. **Isotomodes** Linnaniemi, 1907 (26 spp.) (see Gama 1963; Jordana and Arbea 1990a; Lucianez and Simon 1993b; Simon and Lucianez 1990a)
43. **Isotomurus** Börner, 1903 (48 spp.) (see Carapelli *et al.* 1995a,b; Deharveng and Lek 1993; Lee *et al.* 1993; Poinot-Balaguer 1976)
44. **Jestella** Najt, 1978 (1 sp.)
45. **Martynovella** Deharveng, 1979 (2 spp.)
46. **Metisotoma** Maynard, 1951 (2 spp.)
47. **Micranurophorus** Bernard, 1977 (2 spp.) (see Christian 1986c)
48. **Micrisotoma** Bellinger, 1952 (1 sp.)
49. **Mucracanthus** Stebaeva, 1976 (2 spp.)
50. **Mucrotoma** Rapoport and Rubio, 1963 (1 sp.)
51. **Myopia** Christiansen and Bellinger, 1980 (1 sp.)
52. **Narynia** Martynova, 1968 (3 spp.)
53. **Neocryptopygus** Salmon, 1965 (1 sp.) (see Lawrence 1978b)
54. **Octodontophora** *Chelnokov*, 1990 (1 sp.)
55. **Pachyotoma** Bagnall, 1949 (10 spp.)
56. **Panchaetoma** Bagnall, 1949 (2 spp.)
57. **Papillomurus** Salmon, 1941 (8 spp.)
58. **Paracerura** *Deharveng and Oliveira*, 1994 (2 spp.)
59. **Paranurophorus** Denis, 1929 (1 sp.)
60. **Parisotoma** Bagnall, 1940 (31 spp.) (see Potapov 1989, 1991b)
61. **Pecten isotoma** *Gruia*, 1983 (1 sp.)
62. **Pentacanthella** Deharveng, 1979 (1 sp.)
63. **Procerura** Salmon, 1941 (6 spp.) (see Greenslade 1989)
64. **Proctostephanus** Börner, 1902 (5 spp.) (see Lawrence and Khaloyan 1977; Poinot and Dallai 1970)
65. **Proisotoma** Börner, 1901 (85 spp.) (see Dunger 1987; Ellis 1970; Fjellberg 1973c, 1991a; Lucianez and Simon 1992e)
66. **Proisotomurus** Womersley, 1934 (5 spp.)
67. **Psammisotoma** *Greenslade and Deharveng*, 1986 (3 spp.) (see Thibaud 1993a)
68. **Pseudanurophorus** Stach, 1922 (16 spp.)
69. **Pseudisotoma** Handschin, 1924 (6 spp.)
70. **Pseudofolsomia** Martynova, 1967 (2 spp.)
71. **Pseudosorensia** Izarra, 1972 (3 spp.)

72. **Pteronychella** Börner, 1909 (4 spp.) (see Yoshii 1990)
73. **Rhodanella** Salmon, 1945 (1 sp.)
74. **Sahacanthella** Potapov and Stebaeva, 1994 (1 sp.)
75. **Salmonia** Baijal, 1958 (1 sp.)
76. **Secotomodes** Potapov, 1988 (2 spp.)
77. **Semicerura** Maynard, 1951 (3 spp.)
78. **Sericeotoma** Potapov, 1991*b* (1 sp.)
79. **Setocerura** Salmon, 1949 (5 spp.) (see Greenslade 1989)
80. **Sibiracanthella** Potapov and Stebaeva, 1994 (1 sp.)
81. **Sibirisotoma** Rusek, 1991*d* (1 sp.)
82. **Spinocerura** Salmon, 1941 (2 spp.) (see Greenslade 1989)
83. **Stachanorema** Wray, 1957 (3 spp.) (see Babenko 1994*b*)
84. **Subisotoma** Stach, 1947 (9 spp.)
85. **Tetracanthella** Schött, 1891 (90 spp.) (see Deharveng 1987*c*; Potapov and Karpus 1993; Potapov and Kuchiev 1993; Rusek 1979*b*; Rusek and Marshall 1976)
86. **Tiancanthella** Rusek, 1979*b* (1 sp.)
87. **Tibiolatras** Salmon, 1941 (1 sp.) (see Greenslade 1989)
88. **Tomocerura** Wahlgren, 1901 (5 spp.) (see Greenslade 1989)
89. **Tuvia** Grinbergs, 1962 (2 spp.)
90. **Uzelia** Absolon, 1901 (11 spp.)
91. **Vertagopus** Börner, 1906 (22 spp.) (see Fjellberg 1978*a*, 1980*c*)
92. **Weberacantha** Christiansen, 1951 (1 sp.) (see Lawrence 1978*b*)
93. **Yosiiella** Hüther, 1967 (1 sp.)

1.2.6 Family MICROFALCULIDAE (1 sp.)

1. **Microfalcula** Massoud and Betsch, 1966 (1 sp.) (see Betsch and Massoud 1973)

1.2.7 Family ONCOPODURIDAE (40 spp.)

1. **Harlomillsia** Bonet 1944 (1 sp.)
2. **Oncopodura** Carle and Lebedinsky, 1905 (39 spp.) (see Christiansen and Reddell 1986; Deharveng 1988*d*; Szeptycki 1977*a,b*; Thibaud and Najt 1987)

1.2.8 Family PARONELLIDAE (336 spp.)

1. **Akabosia** Kinoshita, 1919 (1 sp.)
2. **Bromacanthus** Schött, 1925 (9 spp.) (see Yoshii and Greenslade 1993; Yoshii and Suhardjono 1992*a*)
3. **Callyntrura** Börner, 1906 (89 spp.) (see Lee and Park 1989; Mitra 1974; Yoshii 1982; Yoshii and Greenslade 1993)
4. **Campylothorax** Schött, 1893 (8 spp.) (see Mitra and Dallai 1980)
5. **Cyphoderopsis** Carpenter, 1917 (11 spp.) (see Thibaud and Najt 1988)

6. **Dicranocentroides** Imms, 1912 (15 spp.) (see Yoshii 1982)
7. **Glacialoca** Salmon, 1941 (1 sp.)
8. **Idiomerus** Imms, 1912 (1 sp.)
9. **Lepidonella** Yosii, 1960 (14 spp.) (see Deharveng and Bedos 1995)
10. **Metacoelura** Salmon, 1951 (3 spp.) (see Yoshii and Suhardjono 1992b)
11. **Micronellides** Salmon, 1944 (1 sp.)
12. **Parachaetoceras** Salmon, 1941 (1 sp.)
13. **Paronana** Womersley, 1939 (7 spp.)
14. **Paronella** Schött, 1893 (14 spp.) (see Thibaud and Najt 1988)
15. **Paronellides** Schött, 1925 (10 spp.)
16. **Plumachaetas** Salmon, 1951 (2 spp.)
17. **Pseudoparonella** Handschin, 1925 (19 spp.) (see Yoshii and Suhardjono 1992a)
18. **Pseudoparonellides** Salmon, 1941 (3 spp.)
19. **Pseudosalina** Mitra, 1974 (4 spp.)
20. **Salina** MacGillivray, 1894 (59 spp.) (see Christiansen and Bellinger 1992; Mitra 1973; Yoshii and Suhardjono 1992a)
21. **Troglobius** *Palacios-Vargas and Wilson, 1990* (1 sp.)
22. **Troglopedetes** Absolon, 1907 (29 spp.) (see Deharveng and Gers 1993; Ojeda and Palacios-Vargas 1984; Palacios-Vargas *et al.* 1985; Thibaud and Najt 1988; Wilson 1982)
23. **Trogolaphysa** Mills, 1938 (33 spp.) (see Thibaud and Najt 1988; Yoshii 1988)
24. **Yosiia** Mitra, 1967 (1 sp.)

1.2.9 Family TOMOCERIDAE (115 spp.)

1. **Antennacyrtus** Salmon, 1941 (1 sp.)
2. **Aphaenomurus** Yosii, 1956 (2 spp.)
3. **Lasofinius** *Ireson and Greenslade, 1990* (2 spp.)
4. **Lepidophorella** Schäffer, 1897 (11 spp.)
5. **Lethemurus** Yosii, 1970 (2 spp.)
6. **Millsia** Womersley, 1942 (1 sp.) (see Greenslade 1989)
7. **Monodontocerus** Yosii, 1955 (1 sp.)
8. **Neophorella** Womersley, 1934 (1 sp.) (see Ireson and Greenslade 1990)
9. **Novacerus** Salmon, 1942 (3 spp.)
10. **Plutomurus** Yosii, 1956 (24 spp.) (see Christiansen 1980; Stomp and Weiner 1994; Suma 1981)
11. **Pogonognathellus** Paclt, 1944 (8 spp.) (see Massoud and Ellis 1974)
12. **Tomocerina** Yosii, 1955 (8 spp.)
13. **Tomocerus** Nicolet, 1842 (47 spp.) (see Calandrino 1987; Christiansen 1964b)
14. **Tomolonus** Mills, 1949 (1 sp.) (see Rusek 1977)
15. **Tritomurus** Frauenfeld, 1854 (3 spp.)

2 Order NEELIPLEONA

2.1 Family NEELIDAE (25 spp.)

1. **Megalothorax** Willem, 1900 (17 spp.) (see Christiansen and Bellinger 1992; Deharveng and Beruete 1993)
2. **Neelides** Caroli, 1912 (4 spp.)
3. **Neelus** Folsom, 1896 (3 spp.) (see Massoud and Vannier 1967)
4. **Zelandothorax** Delamare Deboutteville and Massoud, 1963 (1 sp.)

3 Order SYMPHYPLEONA

3.1 Family MACKENZIELLIDAE (1 sp.)

1. **Mackenziella** Hammer, 1953 (1 sp.) (see Fjellberg 1989)

3.2 Family SMINTHURIDAE

3.2.1 Subfamily BOURLETIELLINAE (176 spp.)

1. **Aneuempodialis** Stach, 1955 (2 spp.)
2. **Anjavidiella** Betsch, 1974 (5 spp.) (see Betsch 1980)
3. **Bourletides** Betsch and Massoud, 1972 (1 sp.)
4. **Bourletiella** Banks, 1899 (19 spp.) (see Bretfeld 1990, 1994c; Fjellberg 1984d; Nayrolles 1988, 1989b, 1990a,b, 1991; Snider 1981d)
5. **Bourletielitas** Betsch, 1974 (1 sp.)
6. **Bovicornia** Delamare Deboutteville, 1947 (7 spp.) (see Dallai 1981; Massoud and Delamare Deboutteville 1964)
7. **Cassagnaudiella** Ellis, 1975 (9 spp.) (see Nayrolles 1995b)
8. **Corynephoris** Absolon, 1907 (7 spp.) (see Greenslade 1977)
9. **Cyprania** Bretfeld, 1992b (1 sp.) (see Nayrolles 1993c)
10. **Deuterosminthurus** Börner, 1901 (30 spp.) (see Bretfeld 1990; Christiansen and Bellinger 1992; Nayrolles 1991; Palacios-Vargas and Gonzalez 1995)
11. **Fasciosminthurus** Gisin, 1960 (16 spp.) (see Bretfeld 1992a; Nayrolles 1993c, 1994c)
12. **Heterosminthurus** Stach, 1955 (18 spp.) (See Bretfeld 1990; Christiansen and Bellinger 1992; Snider and Calandrino 1987)
13. **Kaszabellina** Betsch, 1977 (3 spp.)
14. **Massoudia** Betsch, 1975 (1 sp.)
15. **Nasosminthurus** Stach, 1955 (4 spp.)
16. **Parabourletiella** Betsch, 1975 (1 sp.)
17. **Prorastriones** Delamare Deboutteville, 1947 (29 spp.) (see Bretfeld 1990, 1992b; Nayrolles 1987, 1993c; Nayrolles and Lienhard 1990)
18. **Pseudobourletiella** Stach, 1956 (1 sp.)
19. **Rastriones** Börner, 1906 (13 spp.) (see Yoshii and Suhardjono 1992b)
20. **Stenognathiones** Betsch and Lasebikan, 1980 (4 spp.)
21. **Tritosminthurus** Snider, 1988b (1 sp.)

22. **Vatomadiella** Betsch, 1974 (3 spp.) (see Betsch 1980)

3.2.2 *Subfamily DICYRTOMINAE (161 spp.)*

1. **Bothriovulsus** Richards, 1968 (3 spp.) (see Betsch and Weiner 1987; Weiner and Betsch 1992)
2. **Calvatomina** Yosii, 1966 (34 spp.) (see Snider 1990a)
3. **Dicyrtoma** Bourlet, 1842 (23 spp.) (see Soto-Adames 1988a)
4. **Dicyrtomina** Börner, 1903 (18 spp.) (see Nayrolles 1988, 1989a, 1990a,b, 1991; Snider 1990b)
5. **Gibberathrix** Uchida, 1952 (1 sp.)
6. **Papirioides** Folsom, 1924 (8 spp.) (see Greenslade 1994b; Itoh and Zhao 1993b; Snider 1990a)
7. **Ptenothrix** Börner, 1906 (74 spp.) (see Nayrolles 1989a, 1991; Snider 1985a,d, 1990a,b; Yosii and Lee 1963)

3.2.3 *Subfamily KATIANNINAE (241 spp.)*

1. **Arrhopalites** Börner, 1906 (73 spp.) (see Christiansen 1966; Nayrolles 1988, 1989b, 1990a,b,c; 1991)
2. **Betschurinus** Dallai and Martinozzi, 1980 (1 sp.)
3. **Collophora** Richards, 1964 (6 spp.) (see Dallai and Mohamed 1981; Delamare Deboutteville and Massoud 1964b)
4. **Dalianus** Cassagnau, 1969 (1 sp.) (see Nayrolles 1991)
5. **Gisinianus** Betsch, 1977 (1 sp.)
6. **Katianna** Börner, 1906 (42 spp.) (see Snider 1989)
7. **Katiannellina** Delamare Deboutteville and Massoud, 1963 (1 sp.)
8. **Katiannina** Maynard and Downs, 1951 (1 sp.)
9. **Millsurus** Betsch, 1977 (1 sp.)
10. **Neokatianna** Snider, 1989 (1 sp.)
11. **Parakatianna** Womersley, 1932 (13 spp.)
12. **Polykatianna** Salmon, 1946 (11 spp.) (see Snider 1969b, 1988a)
13. **Pseudokatianna** Salmon, 1944 (14 spp.)
14. **Rusekianna** Betsch, 1977 (1 sp.)
15. **Sminthurinus** Börner, 1901 (68 spp.) (see Nayrolles 1988, 1989b, 1990a,b, 1991; Snider 1989)
16. **Stenognathellus** Stach, 1956 (5 spp.)
17. **Zebulonia** Betsch, 1970 (1 sp.)

3.2.4 *Subfamily SMINTHURIDINAE (126 spp.)*

1. **Debouttevillea** Murphy, 1965 (1 sp.)
2. **Denisiella** Folsom and Mills, 1938 (6 spp.) (see Palacios-Vargas 1995; Snider 1988c)
3. **Jeannenotia** Stach, 1956 (1 sp.) (see Betsch and Massoud 1970)
4. **Pygicornides** Betsch, 1969 (2 spp.) (see Betsch and Massoud 1972)
5. **Sinnamarides** Betsch and Waller, 1991 (1 sp.)

6. **Sminthurides** Börner, 1900 (55 spp.) (see Dunger and Fritzlar 1986; Nayrolles 1988, 1989*b*, 1990*a,b*, 1991; Yoshii and Suhardjono 1992*b*)
7. **Sminthuridia** Massoud and Betsch, 1972 (1 sp.)
8. **Sphaeridia** Linnaniemi, 1912 (52 spp.) (see Bretfeld and Gauer 1994; Dunger and Bretfeld 1989; Nayrolles 1989*b*, 1990*b*, 1991)
9. **Stenacidia** Börner, 1906 (3 spp.) (see Betsch and Massoud 1970)
10. **Yosiides** Massoud and Betsch, 1972 (2 spp.) (see Itoh and Zhao 1993*a*)

3.2.5 Subfamily SMINTHURINAE (181 spp.)

1. **Afrosminthurus** Delamare Deboutteville and Massoud, 1964 (2 spp.)
2. **Allacma** Börner, 1906 (4 spp.) (see Fanciulli *et al.* 1994; Nayrolles 1994*a*)
3. **Austrosminthurus** Delamare Deboutteville and Massoud, 1963 (1 sp.)
4. **Caprainea** Dallai, 1970 (3 spp.) (see Nayrolles 1991, 1993*b*)
5. **Cordobaia** Simon *et al.* 1987 (1 sp.)
6. **Disparrhopalites** Stach, 1956 (1 sp.) (see Dallai 1970*a*)
7. **Gisinurus** Dallai, 1970 (1 sp.) (see Nayrolles 1993*b*)
8. **Lipothrix** Börner, 1906 (3 spp.) (see Itoh 1994*b*; Nayrolles 1990*b*, 1991, 1993*b*)
9. **Neosminthurus** Mills, 1934 (9 spp.) (see Muzzio 1984)
10. **Novokatianna** Salmon, 1944 (3 spp.)
11. **Papirinus** Yosii, 1954 (4 spp.)
12. **Pararrhopalites** Bonet and Tellez, 1949 (7 spp.)
13. **Parasphyrotheca** Salmon, 1951 (4 spp.)
14. **Richardasita** Betsch, 1975 (2 spp.)
15. **Sminthurus** Latreille, 1802 (73 spp.) (see Itoh 1985; Nayrolles 1988, 1989*b*, 1990*a,b*, 1991, 1995*c*; Snider 1981*b*, 1982*a,b*, 1983*b*, 1985*c*; Snider and Loring 1982)
16. **Songhaica** Lasebikan *et al.*, 1980 (2 spp.)
17. **Spatulosminthurus** Betsch and Betsch-Pinot, 1983 (7 spp.) (see Nayrolles 1990*d*, 1994*a*)
18. **Sphyrotheca** Börner, 1906 (21 spp.) (see Christiansen and Bellinger 1992; Itoh and Zhao 1993*a*)
19. **Temeritas** Delamare Deboutteville and Massoud, 1963 (29 spp.) (see Betsch 1971, 1980; Dallai and Fanciulli 1985)
20. **Vesicephalus** Richards, 1964 (4 spp.) (see Ardanaz and Pozo 1985; Delamare Deboutteville and Massoud 1964*a*; Snider 1985*b*)

3.2.6 Subfamily SPINOTHECINAE (4 spp.)

1. **Adelphoderia** Greenslade, 1982 (1 sp.) (see Greenslade 1982*b*)
2. **Spiniotheca** Stach, 1956 (3 spp.)

3.2.7 Subfamily STURMINAE (1 sp.)

1. **Sturmius** Bretfeld, 1994*a* (1 sp.)

Appendix B

Regional checklists of Collembola

This appendix contains citations to checklists of the Collembola fauna of the world which (with a few exceptions) have been published since Salmon (1964). Salmon's *Index* contained localities for every species that had been described at the time and this should be consulted for earlier references. The list below is not exhaustive although I have endeavoured to include all the main works. Some references are to studies on specific families, comprehensive ecological surveys of the local springtail fauna or, in a few cases, single species descriptions if they include interesting biogeographical information. The list is designed to facilitate access to the literature on the world distribution of Collembola which is scattered over a very wide range of journals and books. References in italics refer to caves (see also Section 9.6).

Arctic and Holarctic

Devon Island (Northwest Territories, Canada): Babenko (1994a)

Canadian Arctic: Danks (1981), Fjellberg (1986b)

Northern Holarctic: Fjellberg (1986a)

Northern Arctic: Maclean *et al.* (1978)

Norwegian Arctic: Fjellberg (1984a, 1994)

North America

North America: *Christiansen (1982a)*, Christiansen and Bellinger (1980, 1988)

United States: *Christiansen and Culver (1987)*, *Peck and Christiansen (1990)*

Alaska: Fjellberg (1985b), Skidmore (1995)

Canada: Baumbrough *et al.* (1992), Behan-Pelletier (1993), Skidmore (1995) Toda and Tanno (1983)

South and Central America

Neotropics: Mari Mutt and Bellinger (1990), Palacios-Vargas (1989, 1990b), *Yoshii (1988)*

Mexico: *Christiansen (1982b)*, *Christiansen and Culver (1987)*, *Christiansen and Reddell (1986)*, Palacios-Vargas (1981, 1983a, 1983b, 1993, 1994), Palacios-Vargas and Gomez-Anaya (1993), Terron-Sierra and Palacios-Vargas (1991), Vasquez and Palacios-Vargas (1990), Villalobos (1990)

Nicaragua: Maes and Palacios-Vargas (1988)

Costa Rica: Palacios-Vargas (1992*b*)

Panama: Palacios-Vargas (1992*b*)

French Guyana: Betsch and Waller (1991), Betsch and Cancela da Fonseca (1995)

Ecuador: Najt and Thibaud (1987), Najt *et al.* (1988), Thibaud and Najt (1987, 1988, 1989)

Surinam: Delamare-Deboutteville and Massoud (1964*c*)

Argentina: *Palacios-Vargas* (1992*a*)

Venezuela: Diaz and Najt (1994)

Brazil: *Palacios-Vargas and Gnaspini-Netto* (1992)

West Indies

Cuba: *Gruia* (1984), Palacios-Vargas and Diaz (1992), Thibaud (1994*b*)

Jamaica: Betsch (1965*a*), Massoud and Bellinger (1963)

Lesser Antilles: Lescure *et al.* (1991), Massoud and Thibaud (1980, 1987), Thibaud (1991*a*, 1993*a*), Thibaud and Massoud (1979, 1983*b*), Thibaud and Najt (1992)

Atlantic Islands

Macaronesia: Gama (1986*a*)

Canary Islands: Fjellberg (1991*e*, 1995*a*), Gama (1988*c*)

Tristan da Cunha: Rapoport (1969*b*)

St. Helena: Lawrence (1970*b*)

Europe

Europe: Deharveng and Thibaud (1989*a*), Gisin (1957, 1958, 1960*a,c*, 1962*c*, 1963*b*, 1964*a,b*), Thibaud and Massoud (1973*a*)

Scandinavia: Hipa *et al.* (1988)

Faroe Islands: Bödvarsson (1960*b*)

Iceland: Bödvarsson (1966, 1967)

Sweden: Bödvarsson (1973)

Norway: Fjellberg (1976*e,f*, 1980*a*, 1988*a*), Hågvar (1982, 1983)

United Kingdom: Gough (1978), Hale (1963, 1966*a*), Hazelton (1972), Kloet and Hinks (1964), Lawrence (1959), Wood (1967*a,b,c*)

Ireland: Bolger (1986), Curry (1969), *Hazelton* (1974*a,b,c*)

France: *Christiansen and Bouillion* 1978*a,b*; *Deharveng* (1979*a*, 1986*c*, 1988*c,d*, 1989*a*), *Deharveng and Beruete* (1993), *Deharveng and Gouze* (1984, 1986), Pichard *et al.* (1989), Ponge (1993), Prat and Massoud (1980, 1981, 1982), *Stomp et al.* (1982), Thibaud (1995*a*), *Thibaud and Stomp* (1978)

Corsica: Poinot (1972)

Iberian Peninsula: Arbea and Jordana (1991*b*), Jordana and Arbea (1989*c*), Jordana *et al.* (1990), Selga (1971)
 Spain: Gama (1984*b*, 1985), Jordana and Beruete (1983)
 Portugal: Gama (1964), Gama *et al.* (1989*b*)
 Balearic Islands: Arbea and Jordana (1990*b*)
 Belgium: André (1983, 1985), Berbiers and Segers (1991), Thibaud and Massoud (1977)
 Netherlands: Vegter (1983), Vegter *et al.* (1988*a,b*)
 Germany: Böhle (1991), Fritsch (1992), Gerdsmeyer and Greven (1987, 1991*a,b*, 1992), Schaefer and Schauerermann (1990), Schultz (1994), Wolters (1983)
 Hiddensee Island (Germany): Schultz (1991)
 Austria: Bretschko and Christian (1989), Christian (1985*a*, 1986*b,c*, 1987), Christian and Thibaud (1988), Deharveng (1986*b*, 1987*e*), Haybach (1992), Kampichler (1992), Kopeszki and Jandl (1994), Kopeszki and Meyer (1994), Stomp *et al.* (1991), Thibaud and Christian (1986)
 Hungary: Christian and Thibaud (1988), Thibaud and Christian (1991), Traser *et al.* (1993)
 Bulgaria: Thibaud (1984*b*)
 Romania: Thibaud (1992)
 Poland: Pomorski (1992*b*), Pomorski and Skarzynski (1992), Stach (1964*b*), Szeptycki (1967*b*), Szeptycki and Weiner (1990), Thibaud and Weiner (1994), Weiner (1981)
 ‘Czechoslovakia’: Kovác (1994), Rusek (1989*b*), Rusek *et al.* (1975)
 ‘Yugoslavia’: Barra (1993), Palissa and Zivadinovic (1974)
 Albania: Thibaud (1992), Thibaud and Peja (1994)
 Italy: Dallai and Malatesta (1982), Dallai *et al.* (1995)
 Italian islands: Dallai (1968, 1969*a,b*)
 Crete: Ellis (1976)
 Malta: Stach (1967)
 Rhodes: Ellis (1974*a*)
 North Adriatic coast: Christian (1989*a*)
 Mediterranean coast: Thibaud and Christian (1989)

Africa

North Africa: Stomp (1974, 1983), Thibaud (1984*a*)
 Morocco: Gers and Deharveng (1985), Thibaud and Massoud (1980)
 Nigeria: Betsch and Lasebikan (1979)
 Cameroon: Cassagnau (1991*a*)
 Gabon: Barra (1969*b*)
 Angola: Gama (1966), Massoud (1964*b*)
 Kenya: Deharveng and Diaz (1984)
 South Africa: Barra (1994), Coates (1968*a,b*, 1969), Paclt (1967), Weiner and Najt (1991*b*)
 Madagascar: Betsch (1970, 1974*a,b*, 1975*a*), Palacios-Vargas and Wilson (1990)

Asia

Former Soviet Union: Ananeva *et al.* (1987), Babenko (1993), Babenko *et al.* (1994), Budaeva (1993), Bulavintsev and Babenko (1989), Martynova (1964)
Afghanistan: Stach (1960*b*, 1963*b*), Yosii (1966*a*)
Iraq: Rusek (1981)
Iran: Cox (1982)
India: Prabhoo (1971*a,b*), Salmon (1970*b*), Yosii (1966*a*)
Sri Lanka: Cassagnau (1988, 1991*b*), Yosii (1966*a*)
Mongolia: Betsch (1977*d*), Dunger (1978*a*, 1982, 1983)
Himalayan region: Cassagnau (1981, 1990*b*, 1991*c*, 1993*a,b,c*), Yosii (1966*d*, 1971*b*)

Orient

China: Chen and Christiansen (1993), Itoh and Zhao (1993*a,b*), Li (1992), Stach 1964*b*)
Taiwan: Lee and Kim (1990), Lee and Park (1989)
North and South Korea: Deharveng and Weiner (1984), Lee (1973, 1974*a,b*, 1974*c*, 1975, 1977), Lee and Choe (1979) Lee and Kim (1984, 1994, 1995*a,b*), Lee and Park (1984, 1986, 1992), Lee and Thibaud (1975), Lee *et al.* (1993), Najt and Weiner (1985, 1992), Szeptycki (1973, 1977*b*), Thibaud (1993*b*), Thibaud and Lee (1994), Weiner (1986*b*, 1989*b*, 1994), Weiner and Betsch (1992), Weiner and Najt (1985*a,b*)
Japan: Sugawara *et al.* (1987), Takeda (1976, 1978, 1979*a,c*), Uchida (1971, 1972*a,b*), Yosii (1956*a,b*, 1965, 1967*b*, 1970, 1971*a*, 1977)

South-East Asia

South-East Asia: Deharveng (1987*a*), Deharveng and Leclerc (1989)
Vietnam: Deharveng and Bedos (1995), Stach (1965)
Thailand: Bedos and Deharveng (1990, 1994), Deharveng (1986*d*, 1988*e*, 1990), Deharveng and Bedos (1993*a,b*), Deharveng and Bourgeois (1991), Deharveng and Gers (1993), Deharveng *et al.* (1989), Koo and Deharveng (1990), Nayrolles (1990*c*)
Indonesia: Deharveng (1989*d*), Deharveng and Suhardjono (1994), Suhardjono (1989*a,b*), Yosii and Suhardjono (1989)
Java: Gunadi (1994)
Sulawesi: Deharveng (1987*e*), Yoshii and Greenslade (1993)
Papua New Guinea: Deharveng (1980*c*, 1982*c*, 1983*b*)
Solomon Islands: Deharveng and Greenslade (1990), Greenslade and Greenslade (1980), Lawrence (1969*a*), Yosii (1969)
Philippines: Cassagnau and Deharveng (1984), Gapud (1971)

Australasia

New Caledonia: Deharveng (1988*a*), Deharveng and Najt (1989), Guilbert *et al.* (1995), Najt and Weiner (1991), Weiner (1991*b*), Weiner and Najt (1991*a*), Yoshii (1989*b*)

Australia: Greenslade (1991*a*, 1992*a*, 1993, 1994*a*), Greenslade and Crawford (1994); Greenslade and Greenslade (1989), Greenslade and Mott (1982), Greenslade and Thompson (1981), Greenslade *et al.* (1991), Hutson and Veitch (1983, 1987), Yoshii and Greenslade (1994)
Kangaroo Island: Greenslade (1974)
New Zealand: Salmon (1970*a*), Wise (1977)

Pacific Islands

Hawaii: Bellinger and Christiansen (1974, 1989), Christiansen and Bellinger (1992, 1994), Snider (1990*a*)
Tonga: Yosii (1964)
Galapagos Islands: Najt *et al.* (1991), Thibaud *et al.* (1994)
Fangataufa: Thibaud and Najt (1993)

Antarctica

Antarctic: Block (1992), Booth and Usher (1984), Wise (1967, 1971)
Macquarie Island: Greenslade and Van Klinken (1994), Greenslade and Wise (1986)
Heard Island: Greenslade (1986*b*, 1995); Wise (1970*b*)
Bouvetøya: Sømme (1986*b*)
South Georgia: Wise (1970*a*)
South Shetland Islands: Richard *et al.* (1994)

Appendix C

Laboratory and field studies on the effects of chemicals on Collembola

The table below lists citations to laboratory (L) and field studies (F) on the accumulation and effects of a range of inorganic and organic chemicals on Collembola (see also Thompson and Gore (1972) who tested 29 insecticides on *Folsomia candida*).

Metals

Cadmium	<i>Folsomia candida</i>	Crommentuijn <i>et al.</i> (1993, 1994, 1995)	L
	<i>Isotoma notabilis</i>	Van Straalen and Van Wensem (1986)	F
	<i>Lepidocyrtus cyaneus</i>	Van Straalen and Van Wensem (1986)	F
	<i>Orchesella cincta</i>	Janssen and Bedaux (1989)	F
	<i>Orchesella cincta</i>	Janssen and Bergema (1991)	L
	<i>Orchesella cincta</i>	Janssen and Hogerworst (1993)	F
	<i>Orchesella cincta</i>	Janssen <i>et al.</i> (1990, 1991)	L,F
	<i>Orchesella cincta</i>	Posthuma (1990)	L, F
	<i>Orchesella cincta</i>	Posthuma <i>et al.</i> (1992, 1993a,b)	L, F
	<i>Orchesella cincta</i>	Rabitsch (1995)	F
	<i>Orchesella cincta</i>	Van Straalen and De Goede (1987)	L
	<i>Orchesella cincta</i>	Van Straalen and Van Wensem (1986)	F
	<i>Orchesella cincta</i>	Van Straalen <i>et al.</i> (1986, 1987, 1989)	L,F
	<i>Pogonognathellus longicornis</i>	Rabitsch (1995)	F
	Pooled sample	Hunter <i>et al.</i> (1987)	F
Copper	<i>Orchesella cincta</i>	Janssen and Hogerworst (1993)	F
	<i>Orchesella cincta</i>	Rabitsch (1995)	F
	<i>Orchesella cincta</i>	Van Straalen <i>et al.</i> (1987)	L, F
	<i>Pogonognathellus longicornis</i>	Rabitsch (1995)	F
	<i>Protaphorura armata</i>	Bengtsson and Rundgren (1988)	
	<i>Protaphorura armata</i>	Bengtsson <i>et al.</i> (1983, 1985a)	
	Pooled sample	Hunter <i>et al.</i> (1987)	F
	Various	Filser (1995a)	F
	Various	Filser <i>et al.</i> (1995)	F
	Various	Parmelee <i>et al.</i> (1993)	L

Copper/ zinc	<i>Folsomia fimetarioides</i>	Bengtsson <i>et al.</i> (1994a)	L
	<i>Folsomia fimetarioides</i>	Tranvik and Eijsackers (1989)	L
	<i>Isotoma notabilis</i>	Tranvik <i>et al.</i> (1993)	L
	<i>Isotomiella minor</i>	Bengtsson <i>et al.</i> (1994a)	L
	<i>Isotomiella minor</i>	Tranvik and Eijsackers (1989)	L
	<i>Protaphorura armata</i>	Tranvik <i>et al.</i> (1993)	L
	<i>Protaphorura armata</i>	Bengtsson and Rundgren (1988)	F
	<i>Protaphorura armata</i>	Bengtsson <i>et al.</i> (19885b)	L
Iron	<i>Orchesella cincta</i>	Janssen and Hogerworst (1993)	F
Iron/ manganese	<i>Orchesella cincta</i>	Nottrot <i>et al.</i> (1987)	L
Manganese	<i>Orchesella cincta</i>	Janssen and Hogerworst (1993)	F
Lead	<i>Entomobrya nivalis</i>	Roth (1993)	F
	<i>Isotoma notabilis</i>	Van Straalen and Van Wensem (1986)	F
	<i>Lepidocyrtus cyaneus</i>	Van Straalen and Van Wensem (1986)	F
	<i>Lepidocyrtus lignorum</i>	Roth (1993)	F
	<i>Orchesella cincta</i>	Janssen and Hogerworst (1993)	F
	<i>Orchesella cincta</i>	Joesse and Buker (1979)	L
	<i>Orchesella cincta</i>	Joesse and Verhoef (1983)	L
	<i>Orchesella cincta</i>	Rabitsch (1995)	F
	<i>Orchesella cincta</i>	Van Straalen (1987)	L, F
	<i>Orchesella cincta</i>	Van Straalen and Van Meerendonk (1987)	L
	<i>Orchesella cincta</i>	Van Straalen and Van Wensem (1986)	F
	<i>Orchesella cincta</i>	Van Straalen <i>et al.</i> (1985, 1986, 1987)	L, F
	<i>Orchesella flavescens</i>	Roth (1993)	F
	<i>Pogonognathellus longicornis</i>	Rabitsch (1995)	F
	<i>Protaphorura armata</i>	Bengtsson and Rudgren (1988)	F
	<i>Protaphorura armata</i>	Bengtsson <i>et al.</i> (1983, 1985a)	L
	<i>Tomocerus minor</i>	Roth (1993)	F
	Various	Hågvar and Abrahamsen (1990)	F
	Various	Kronshage (1992)	L
Tin	<i>Folsomia candida</i>	Crommentuijn <i>et al.</i> (1995)	L
(TPT-OH)	<i>Isotoma notabilis</i>	Van Straalen and Van Wensem (1986)	F
Zinc	<i>Lepidocyrtus cyaneus</i>	Van Straalen and Van Wensem (1986)	F
	<i>Orchesella cincta</i>	Janssen and Hogerworst (1993)	F
	<i>Orchesella cincta</i>	Posthuma (1990)	L, F
	<i>Orchesella cincta</i>	Van Straalen and Van Wensem (1986)	F
	<i>Orchesella cincta</i>	Rabitsch (1995)	F
	<i>Orchesella cincta</i>	Van Straalen <i>et al.</i> (1987)	L, F
	<i>Pogonognathellus longicornis</i>	Rabitsch (1995)	F
	Various	Strojan (1978)	F
Various	Various	Lübben (1989)	F
(in sludge)	Various	Lübben and Larink (1990)	F

Herbicides

Atrazine	<i>Folsomia candida</i>	Subagja and Snider (1981)	L
	<i>Onychiurus apuanicus</i>	Mola <i>et al.</i> (1987)	L
	<i>Orchesella cincta</i>	Badejo and Van Straalen (1992)	L
	<i>Protaphorura armata</i>	Mola <i>et al.</i> (1987)	L
	<i>Tullbergia granulata</i>	Subagja and Snider (1981)	L
	Various	Fratello <i>et al.</i> (1985, 1986)	F
	Various	Mallow <i>et al.</i> (1985)	F
	Various	Moore <i>et al.</i> (1984)	F
	Various	Popovici <i>et al.</i> (1977)	F
	Various	Wardle <i>et al.</i> (1993)	F
Bromacil	Various	Wardle <i>et al.</i> (1993)	F
Caragard	Various	Wardle <i>et al.</i> (1993)	F
Hexazinone	Various	Badejo and Adejuyigbe (1994)	F
MCPB	Various	Wardle <i>et al.</i> (1993)	F
Nitrofen	Various	Parmelee <i>et al.</i> (1993)	L
Paraquat	<i>Folsomia candida</i>	Subagja and Snider (1981)	L
	<i>Tulbergia granulata</i>	Subagja and Snider (1981)	L
Rimsulfuron	Various	Wardle <i>et al.</i> (1993)	F
2,4,5-T	<i>Protaphorura</i>	Eijsackers (1975, 1978a,b)	L
	<i>quadriocellata</i>		
Various	Various	Büchs (1994)	F

Fungicides

Aktuan	Various	Filser (1994)	F
Benomyl	Various	Tomlin (1975, 1977)	L
	Various	Krogh (1991)	F
Carbendazim	<i>Sminthurinus aureus</i>	Frampton (1988a)	L
Pentachlorophenate	<i>Folsomia candida</i>	Gruttke <i>et al.</i> (1988)	L
Propiconazole	<i>Sminthurinus aureus</i>	Frampton (1988a)	L
Pyrizophos	<i>Sminthurinus aureus</i>	Frampton (1988a,b)	L
Triadimenol	<i>Sminthurinus aureus</i>	Frampton (1988a)	L

Organochlorine insecticides

Aldrin	<i>Protaphorura hortensis</i>	Edwards (1962)	
	Various	Edwards <i>et al.</i> (1967)	F
	Various	Joy and Chakravorty (1991)	L, F
Chlordane	Various	Joy and Chakravorty (1991)	L, F
DDT	<i>Folsomia candida</i>	Butcher <i>et al.</i> (1969)	L
	Various	Edwards <i>et al.</i> (1967)	F
	Various	Knight and Chesson (1966)	F

	Various	Lupetti <i>et al.</i> (1994)	F
	Various	Perfect <i>et al.</i> (1981)	F
Dieldrin	<i>Folsomia candida</i>	Thompson (1973)	L
Endosulfan	Various	Filser (1990)	L, F
	Various	Fromm and Filser (1991)	L
	Various	Joy and Chakravorty (1991)	L, F
Isobenzan	<i>Folsomia candida</i>	Thompson (1973)	L
Lindane	<i>Protaphorura hortensis</i>	Edwards (1962)	F
	Various	Czarnecki and Losinski (1985)	F
	Various	Grégoire-Wibo (1983)	F

Organophosphorous insecticides

Chlorpyrifos	<i>Folsomia candida</i>	Crommentuijn <i>et al.</i> (1995)	L
	<i>Folsomia candida</i>	Thompson (1973)	L
	<i>Folsomia candida</i>	Wiles and Frampton (1996)	L, F
	<i>Isotoma viridis</i>	Wiles and Frampton (1996)	L, F
	<i>Isotomurus palustris</i>	Wiles and Frampton (1996)	L, F
	<i>Sminthurus viridis</i>	Wiles and Frampton (1996)	L, F
	Various	Stark (1992)	F
	Various	Wilson <i>et al.</i> (1995)	F
Diazinon	<i>Bourletiella hortensis</i>	Marshall and Ilnytzky (1976)	F
	<i>Folsomia candida</i>	Thompson (1973)	L
Dimethoate	<i>Folsomia candida</i>	Krogh (1995a)	L
	<i>Folsomia fimetaria</i>	Krogh (1995a)	L
	<i>Folsomia fimetaria</i>	Fabian and Petersen (1994)	L
	Various	Joy and Chakravorty (1991)	L, F
Fensulfothion	Various	Tomlin (1975)	L
Fonofos	<i>Bourletiella hortensis</i>	Marshall and Ilnytzky (1976)	F
Isofenphos	Various	Krogh (1991)	F
Malathion	<i>Bourletiella hortensis</i>	Marshall and Ilnytzky (1976)	F
Methyl-parathion	Various	Joy and Chakravorty (1991)	L, F
Monocrotophos	Various	Joy and Chakravorty (1991)	L, F
Phorate	<i>Folsomia candida</i>	Thompson (1973)	L
Phosphamidon	Various	Joy and Chakravorty (1991)	L, F
Zinophos	<i>Folsomia candida</i>	Thompson (1973)	L
Various	<i>Folsomia candida</i>	Grimnes (1986)	L
	Various	Wibo (1973)	F

Carbamate insecticides

Aldicarb	Various	Grégoire-Wibo (1983)	F
Carbaryl	Various	Joy and Chakravorty (1991)	L, F

	Various	Wilson <i>et al.</i> (1995)	F
Carbofuran	<i>Folsomia candida</i>	Thompson (1973)	L
Methomyl	Various	Filser and Nagel (1993)	L, F
Oxamyl	<i>Bourletiella hortensis</i>	Marshall and Illnysitzky (1976)	F
Pirimicarb	<i>Folsomia candida</i>	Wiles and Frampton (1996)	L, F
	<i>Isotoma viridis</i>	Wiles and Frampton (1996)	L, F
	<i>Isotomurus palustris</i>	Wiles and Frampton (1996)	L, F
	<i>Sminthurus viridis</i>	Wiles and Frampton (1996)	L, F
Various	Various	Büchs (1994)	F

Synthetic pyrethroids

Cyhalothrin	Various	Filser and Nagel (1993)	L, F
Cypermethrin	<i>Folsomia candida</i>	Wiles and Frampton (1996)	L, F
	<i>Isotoma viridis</i>	Wiles and Frampton (1996)	L, F
	<i>Isotomurus palustris</i>	Wiles and Frampton (1996)	L, F
	<i>Sminthurus viridis</i>	Wiles and Frampton (1996)	L, F

Soil fumigants

Chloropicrin	<i>Protaphorura hortensis</i>	Edwards (1962)	F
Methyl bromide	<i>Protaphorura hortensis</i>	Edwards (1962)	F

Air pollution

'Acid rain'	<i>Folsomia candida</i>	Kopeszki (1992 <i>b</i>)	L, F
	<i>Heteromurus nitidus</i>	Kopeszki (1992 <i>b</i>)	L, F
	<i>Isotoma tigrina</i>	Wolters (1991)	L
	<i>Isotomiella minor</i>	Hågvar (1990)	L
	<i>Mesaphorura yosii</i>	Hågvar (1990)	L
	Various	Hågvar (1984, 1987 <i>a,b</i> , 1988)	L, F
	Various	Hågvar and Abrahamsen (1980)	L, F
	Various	Hågvar and Kjøndal (1981 <i>b</i>)	F
	Various	Heungens and Van Daele (1984)	F
	Various	Kopeszki (1991, 1992 <i>a</i> , 1993 <i>b</i>)	F
	Various	Kronshage (1992)	L
	Various	Rusek (1993)	F
	Various	Van Straalen <i>et al.</i> (1988)	F
	Various	Vilkamaa and Huhta (1986)	F
General	Various	Steiner (1994, 1995)	F

Radiation

Gamma-radiation	Various	Edwards (1969)	L
	Various	Loring (1985)	F
	Various	Poinsot-Balaguer and Tabone (1995)	F
	Various	Poinsot-Balaguer <i>et al.</i> (1991)	F
Caesium -137	Pooled samples	Reichle and Crossley (1965)	F

Miscellaneous

Fertilisers	Various	Kopeszki (1993a)	F
PAHs	<i>Orchesella cincta</i>	Van Straalen <i>et al.</i> (1993)	F
	<i>Orchesella villosa</i>	Van Straalen <i>et al.</i> (1993)	F
PCBs	Various	Lupetti <i>et al.</i> (1994)	F
Phosphate emissions	Various	Fritzlär <i>et al.</i> (1986)	F
Thawing salts	Various	Greven <i>et al.</i> (1991)	F
	Various	Rosgen <i>et al.</i> (1993)	F

References

- Absolon, K. (1900). Vorläufige Mittheilung über einige neue Collembolen aus den Höhlen des mährischen Karstes. *Zoologischer Anzeiger*, **23**, 265–9.
- Absolon, K. (1901). Weitere Nachricht über europäische Höhlencollembolen und über die Gattung *Aphorura* MacGill. *Zoologischer Anzeiger*, **24**, 385–9.
- Adamiec, J. (1975). Ultrastructure of nurse cells in the male gonad of *Tetradontophora bielensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **18**, 85–92.
- Adams, E.C.G. and Salmon, J.T. (1972). The mouth-parts and feeding methods of *Brachystomella parvula* (Schaeffer) (Collembola: Brachystomellidae). *Transactions of the Royal Entomological Society of London*, **124**, 269–86.
- Addison, J.A. (1981). Biology of *Hypogastrura tullbergi* (Collembola) at a high arctic site. *Holarctic Ecology*, **4**, 49–58.
- Agassiz, L. (1842–1846). *Nomenclator zoologicus, continens nomina systematica generum animalium tum viventium quam fossilium*. Jean et Gassman, Solothurn.
- Agrell, I. (1941). Zur Oekologie der Collembolen, untersuchungen in Schwedischen Lappland. *Opuscula Entomologica, Lund*, Supplementum 3, 1–236.
- Agrell, I. (1963). A sociological analysis of soil Collembola. *Oikos*, **14**, 237–47.
- Ågren, H. (1903). Diagnosen einiger neuen Achorutiden aus Schweden (Vorläufige Mittheilung). *Entomologisk Tidskrift*, **24**, 126–8.
- Aitchison, C.W. (1983). Low temperature and preferred feeding by winter active Collembola (Insecta, Apterygota). *Pedobiologia*, **25**, 27–36.
- Aitchison, C.W. (1984). The phenology of Collembola from South Central Canada. *Pedobiologia*, **27**, 405–23.
- Aitchison, C.W. (1986). Provisional notes on a simple method for keeping Collembola. *Pedobiologia*, **29**, 237–8.
- Akam, M., Averof, M., Castelli-Gair, J., Dawes, R., Falciani, F., and Ferrier, D. (1994). The evolving role of Hox genes in arthropods. *Development*, Supplement 1994, 209–15.
- Akkerhuis, G.A.J.M.J. op, Deley, F., Zwetsloot, H.J.C., Ponge, J.F., and Brussaard, L. (1988). Soil microarthropods (Acari and Collembola) in two crop rotations on a heavy marine clay soil. *Revue d'Écologie et de Biologie du Sol*, **25**, 175–202.
- Al-Assiuty, A.I.M., Bayoumi, B.M., Khalil, M.A., and Van Straalen, N.M. (1993). The influence of vegetational type on seasonal abundance and species composition of soil fauna at different localities in Egypt. *Pedobiologia*, **37**, 210–22.
- Aldenberg, T. and Slob, W. (1993). Confidence limits for hazardous concentrations based on logistically distributed NOEC toxicity data. *Ecotoxicology and Environmental Safety*, **25**, 48–63.
- Aldrovandus, U. (1638). *Die animalibus insectis libri septem. I-V Insectis, VI De Vermibus, VII De Aquaticis*. Clement Ferroni, Bologna.
- Alexander, R.Mc.N (1995). Leg design and jumping technique for humans, other vertebrates and insects. *Philosophical Transactions of the Royal Society of London*, **347B**, 235–48.
- Allkin, B. and Winfield, P. (1993). Cataloguing biodiversity: new approaches to old problems. *Biologist*, **40**, 179–83.
- Al-Safadi, M.M. (1988). Observations on the behaviour of *Cryptopygus thermophilus* Axelson (Collembola, Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **25**, 333–41.
- Altner, H. (1988). The scolopidial organs in the first antennal segment in *Allacma fusca* (Collembola, Sminthuridae). *Zoomorphology*, **108**, 173–81.
- Altner, H. and Altner, I. (1985). Multicellular antennal sensilla containing a sensory cell with a short dendrite and dense core granules in the insect *Hypogastrura socialis* (Collembola): intermoult and moulting stages. *Cell and Tissue Research*, **241**, 119–28.
- Altner, H. and Ernst, K.D. (1974). Struktureigentümlichkeiten antennaler Sensillen bodenlebender Collembolen. *Pedobiologia*, **14**, 118–22.
- Altner, H. and Kuhn, K.H. (1989). The terminal antennal sensory complex of Collembola. In *Third International Seminar on Apterygota*, (ed. R. Dallai), pp. 199–206. University of Siena, Siena.

- Altner, H. and Prillinger, L. (1980). Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. *International Review of Cytology*, **67**, 69–139.
- Altner, H. and Thies, G. (1972). Reizleitende Strukturen und Ablauf der Häutung an Sensillen einer euedaphischen Collembolenart. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **129**, 196–216.
- Altner, H. and Thies, G. (1973). A functional unit consisting of an eversible gland with neurosecretory innervation and a proprioceptor derived from a complex sensillum in an insect. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **145**, 503–19.
- Altner, H. and Thies, G. (1976). The postantennal organ: a specialized unicellular sensory input to the protocerebrum in apterygoten insects (Collembola). *Cell and Tissue Research*, **167**, 97–110.
- Altner, H. and Thies, G. (1978). The multifunctional sensory complex in the antenne of *Allacma fusca* (Insecta). *Zoomorphologie*, **91**, 119–31.
- Altner, H. and Thies, G. (1984). Internal proprioceptive organs of the distal antennal segments in *Allacma fusca* (L.) (Collembola: Sminthuridae): proprioceptors phylogenetically derived from sensillum-bound exteroceptors. *International Journal of Insect Morphology and Embryology*, **13**, 315–30.
- Altner, H., Ernst, K.D., and Karuhize, G. (1970). Untersuchungen am Postantennalorgan der Collembolen (Apterygota). I. Die Feinstruktur der postantennalen Sinnesborste von *Sminthurus fuscus* (L.). *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **111**, 263–85.
- Altner, H., Karuhize, G., and Ernst, K.D. (1971). Untersuchungen am Postantennalorgan der Collembolen. II. Cuticulärer Apparat und Dendritenendigung bei *Onychiurus* spec. *Revue d'Écologie et de Biologie du Sol*, **8**, 31–5.
- Ananeva, S.I., Babenko, A.B., and Chernov, Y.I. (1987). Springtails in Arctic tundra of Taimyr. *Zoologicheskoy Zhurnal*, **66**, 1032–44.
- Anderson, J.M. (1988). Invertebrate-mediated transport processes in soils. *Agriculture, Ecosystems and Environment*, **24**, 5–19.
- Anderson, J.M. and Healey, I.N. (1972). Seasonal and inter-specific variations in major components of the gut contents of some woodland Collembola. *Journal of Animal Ecology*, **41**, 359–68.
- Anderson, J.M. and Ineson, P. (1983). Interactions between soil arthropods and microorganisms in carbon, nitrogen and mineral element fluxes from decomposing leaf litter. In *Nitrogen as an Ecological Factor* (ed. J. Lee and S. McNeill), pp. 413–32. Blackwell, Oxford.
- Anderson, J.M. and Ineson, P. (1984). Interactions between microorganisms and soil invertebrates in nutrient flux pathways of forest ecosystems. In *Invertebrate-microbial interactions* (ed. J.M. Anderson, A.D.M. Rayner, and D.W.H. Walton), pp. 59–88. Cambridge University Press.
- André, H.M. (1983). Notes on the ecology of corticolous epiphyte dwellers. *Pedobiologia*, **25**, 271–8.
- André, H.M. (1985). Associations between corticolous microarthropod communities and epiphytic cover on bark. *Holarctic Ecology*, **8**, 113–19.
- André, H.M. (1986). The stases in Collembola: a case study. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 301–5. University of Siena, Siena.
- André, H.M. (1987). The concept of stase in Collembola. In *Soil fauna and soil fertility* (ed. B.R. Striganova), pp. 606–10. Nauka, Moscow.
- André, H.M. (1988a). Redescription of *Xenylla yucatanana* Mills (Collembola: Hypogastruridae). *Folia Entomológica Mexicana*, **74**, 69–77.
- André, H.M. (1988b). The phanerotaxy of the genus *Xenylla* (Collembola: Hypogastruridae), with the description of a new species from Ethiopia. *Journal of African Zoology*, **102**, 503–27.
- André, H.M. (1989a). Some approaches to the study of setae in Collembola. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 33–4. University of Siena, Siena.
- André, H.M. (1989b). The concept of stase. In *Ontogeny and the concept of stase in arthropods* (ed. H.M. André and J.C. Lions), pp. 3–16. AGAR, Wavre, Belgium.
- André, H.M. (1991). Stase, metamorphosis and competition in insects and other arthropods. *Belgian Journal of Zoology*, **121**, 3–25.
- André, H.M., Noti, M.L., and Lebrun, P. (1994). The soil fauna: the other last biotic frontier. *Biodiversity and Conservation*, **3**, 21–8.
- André, O. and Schnürer, J. (1985). Barley straw decomposition with varied levels of microbial grazing by *Folsomia candida* (L.) (Collembola, Isotomidae). *Oecologia*, **68**, 57–62.
- Angermeier, P.L. (1994). Does biodiversity include artificial diversity? *Conservation Biology*, **8**, 600–2.
- Aranda, Y., Serrano, J.M., and Bermudez-de-Castro, F. (1990). Degradacion de la hojarasca de *Populus nigra* L. *Revue d'Écologie et de Biologie du Sol*, **27**, 395–406.
- Arbea, J.I. (1988a). Nuevas especies de *Odontella* (*Superodontella*) (Collembola, Odontellidae) de Navarra (N. de la Péninsula Ibérica). *Miscellanea Zoológica (Barcelona)*, **12**, 109–19.
- Arbea, J.I. (1988b). Nuevas notas taxonómicas sobre las *Odontella* (*Superodontella*) del grupo *lamellifera* (Insecta, Collembola). *Actas III Congreso Ibérico de Entomología, Granada*, 91–104.

- Arbea, J.I. (1989). Colembolos del Moncayo (Zaragoza) (Insecta: Apterygota). II. Ecología de las poblaciones en cuatro parcelas forestales. *Turiaso*, **9**, 585–95.
- Arbea, J.I. (1991). A revision of the genus *Neonaphorura* Bagnall, 1935. *Spixiana*, **14**, 175–88.
- Arbea, J.I. and Jordana, R. (1985a). Efecto de una repoblación con coníferas en un robleal de Navarra sobre los colembolos edáficos. *Boletim da Sociedade Portuguesa Entomologica, Suplemento*, **1**, 277–86.
- Arbea, J.I. and Jordana, R. (1985b). Estudio ecológico de la colembofauna de Los Suelos del Macizo de Quinto Real (Pirineos Occidentales) y descripción de dos especies nuevas: *Anurida flagellata* sp. n. y *Onychiurus subediniensis* sp. n. (Insecta, Collembola). *Boletín de la Estación Central de Ecología, Madrid*, **14**, 57–80.
- Arbea, J.I. and Jordana, R. (1986). Estudio del género *Willemia* en Navarra con especial referencia a la quetotaxia dorsal de la antena (Collembola, Hypogastruridae). *Actas de Las VIII Jornadas A e E, Sevilla*, 213–22.
- Arbea, J.I. and Jordana, R. (1987). Efecto de la repoblación y explotación forestal en la zona norte de Navarra sobre las poblaciones de colembolos edáficos. *Reunión Biología y Ecología del Suelo, Pamplona*, 507–15.
- Arbea, J.I. and Jordana, R. (1988). Nota sobre la presencia masiva de *Onychiurus folsomi* SCHAEFFER (Collembola, Onychiuridae) en lechos de *Eisenia andrei* (Oligochaeta, Lumbricidae). *Bol. San. Veg. Plagas*, **14**, 535–540.
- Arbea, J.I. and Jordana, R. (1989a). The genus *Pseudachorutes* (Collembola, Neanuridae) from Navarra (Northern Iberian Peninsula), with description of a new species and a new subspecies. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **62**, 157–66.
- Arbea, J.I. and Jordana, R. (1989b). Dos nuevas especies de Onychiuridae de Navarra (norte de la Península Ibérica) (Insecta, Collembola). *Eos*, **65**, 7–14.
- Arbea, J.I. and Jordana, R. (1989c). *Friesea cruchagae* n.sp. una nueva especie de Collembola (Neanuridae, Frieseinae). *Boletín de la Asociación Española de Entomología*, **13**, 127–32.
- Arbea, J.I. and Jordana, R. (1990a). Ecología de las poblaciones de colembolos edáficos en un prado y un pinar de la región submediterránea de Navarra. *Mediterranea, Serie Biológicos*, **12**, 139–48.
- Arbea, J.I. and Jordana, R. (1990b). Colembolos de las Islas Baleares (Insecta, Collembola). *Redia*, **73**, 187–200.
- Arbea, J.I. and Jordana, R. (1990c). *Orogastrura octosetosa* n.sp. de los Pirineos atlánticos (Collembola: Hypogastruridae). *Boletín de la Asociación Española de Entomología*, **14**, 17–27.
- Arbea, J.I. and Jordana, R. (1990d). New species of *Pseudosinella* and *Lepidocyrtus* from Navarra (Northern Iberian Peninsula). *Spixiana*, **13**, 25–31.
- Arbea, J.I. and Jordana, R. (1991a). Tres nuevas especies de neanuridos en la Península Ibérica (Collembola, Poduromorpha, Neanuridae). *Graellsia*, **47**, 97–103.
- Arbea, J.I. and Jordana, R. (1991b). Colembolos de Navarra (norte de la Península Ibérica). 1. Orden Poduromorpha (Collembola). *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **22**, 1–149.
- Arbea, J.I. and Jordana, R. (1993). Nuevas especies de *Friesea* Dalla Torre, 1895 de la Península Ibérica (Collembola, Neanuridae). *Boletín de la Real Sociedad Española de Historia Natural, Sección Biológica*, **89**, 5–12.
- Arbea, J.I. and Jordana, R. (1994). Cuatro nuevas especies de la familia Onychiuridae de la Península Ibérica (Collembola, Poduromorpha). *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **24**, 39–59.
- Arbea, J.I. and Lucianez, M.J. (1991). Una nueva especie de *Odontella* (*Superodontella*) Stach, 1949 de la Península Ibérica (Collembola, Odontellidae). *Graellsia*, **47**, 1–5.
- Arbea, J.I. and Mateos, E. (1991). A new species of Collembola from Northern Spain (Onychiuridae, Tullbergiinae). *Spixiana*, **14**, 169–74.
- Arbea, J.I. and Selga, D. (1994). Una nueva subespecie de *Mesaphorura longispina* Arbea & Jordana, 1991 de Barcelona (Collembola, Onychiuridae). *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **24**, 75–9.
- Arbea, J.I. and Weiner, W.M. (1991). Deux nouvelles espèces européennes de *Superodontella* Stach (Collembola, Odontellidae). *Bulletin de la Société Entomologique de France*, **96**, 419–25.
- Arbea, J.I., Urrizalqui, I., and Jordana, R. (1986). Estudio biométrico del género *Protaphorura* en Navarra (Collembola, Onychiuridae). *Actas de Las VIII Jornadas A e E, Sevilla*, 223–34.
- Ardanaz, A. and Jordana, R. (1985). Nuevas especies del género *Pseudosinella* Schäffer en Navarra (España) (Collembola, Entomobryidae). *Boletim da Sociedade Portuguesa Entomologia, Suplemento*, **1**, 261–9.
- Ardanaz, A. and Pozo, J. (1985). Descripción de *Vesicephalus europaeus* n.sp. y primera cita del género para la fauna de Europa. *II Congreso Ibérico de Entomología*, 271–6.

- Argyropoulou, M.D. and Stamou, G.P. (1993). Respiratory activity of the collembolan *Onychiurus meridius*. *Journal of Insect Physiology*, **39**, 217–22.
- Argyropoulou, M.D., Asikidis, M.D., Iatrou, G.D., and Stamou, G.P. (1993). Colonization patterns of decomposing litter in a maquis ecosystem. *European Journal of Soil Biology*, **29**, 183–91.
- Argyropoulou, M.D., Stamou, G.P., and Iatrou, G.D. (1994). Temporal and spatial distribution patterns of Collembola in a patchy environment. *European Journal of Soil Biology*, **30**, 63–9.
- Aritaj, U., Madge, D.S., and Gooderham, P.T. (1977). The effects of compaction of agricultural soils on soil fauna. I. Field investigations. *Pedobiologia*, **17**, 262–82.
- Ashraf, M. (1969). Studies on the biology of Collembola. *Revue d'Écologie et de Biologie du Sol*, **6**, 337–47.
- Averof, M. and Akam, M. (1993). Hom/Hox genes of *Artemia*: implications for the origin of insect and crustacean body plans. *Current Biology*, **3**, 73–8.
- Averof, M. and Akam, M. (1995a). Hox genes and the diversification of insect and crustacean body plans. *Nature*, **376**, 420–3.
- Averof, M. and Akam, M. (1995b). Insect-crustacean relationships: insights from comparative developmental and molecular studies. *Philosophical Transactions of the Royal Society of London*, **347B**, 293–303.
- Avise, J.C. (1994). *Molecular markers, natural history and evolution*. Chapman and Hall, London.
- Axelsson, W.M. (1907). Die apterygotenfauna Finlands. *Acta Societatis Scientiarum Fennicae*, **34**, 1–134.
- Bååth, E. (1991). Tolerance of copper by entomogenous fungi and the use of copper-amended media for isolation of entomogenous fungi from soil. *Mycological Research*, **95**, 1140–2.
- Babel, U. and Vogel, H.J. (1989). Zur Beurteilung der Enchytraeen und Collembolen Aktivitaet mit Hilfe von Bondenduennschliffen. *Pedobiologia*, **33**, 167–72.
- Babenko, A.B. (1993). Temperature preferendum of Collembola species from Arctic tundra of Taimyr. *Entomological Review*, **72**, 89–101.
- Babenko, A.B. (1994a). Collembola in polar desert region of the Devon Island, Canada, NWT. *Entomological Review*, **73**, 134–41.
- Babenko, A.B. (1994b). *Stachanorema tolerans* sp. n. (Collembola; Isotomidae) from the Canadian High Arctic. *Bulletin Entomologique de la Pologne*, **63**, 23–7.
- Babenko, A. and Thibaud, J.M. (1990). Eine neue Hypogastruride (Insecta: Collembola) aus Österreich. *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen*, **42**, 95–6.
- Babenko, A.B., Chernova, N.M., Potapov, M.B., and Stebaeva, S.K. (1994). *Collembola of Russia and adjacent countries: Family Hypogastruridae*. Nauka, Moscow.
- Badejo, M.A. and Adejuyigbe, T.A. (1994). Influence of hexazinone on soil microarthropods in Nigeria. *Fresenius Environmental Bulletin*, **3**, 263–8.
- Badejo, M.A. and Van Straalen, N.M. (1992). Effects of atrazine on growth and reproduction of *Orchesella cincta* (Collembola). *Pedobiologia*, **36**, 221–30.
- Badejo, M.A. and Van Straalen, N.M. (1993). Seasonal abundance of springtails in two contrasting environment. *Biotropica*, **25**, 222–8.
- Bagnall, R.S. (1935). Contributions towards a knowledge of the Scottish Onychiuridae (Collembola), I. *Scottish Naturalist*, July–August 1935, 1111–17.
- Bagnall, R.S. (1937). Contributions towards a knowledge of the Scottish Onychiuridae (Collembola), II. *Scottish Naturalist*, May–June 1937, 87–90, 145–50.
- Bagnall, R.S. (1947). Contributions toward a knowledge of the Onychiuridae (Collembola, Onychiuroidea), I–IV. *Annals and Magazine of Natural History*, Series 11, **14**, 631–42.
- Bagnall, R.S. (1949). Contributions toward a knowledge of the Onychiuridae (Collembola, Onychiuroidea), V–X. *Annals and Magazine of Natural History*, Series 12, **2**, 498–511.
- Baker, A.N. and Dunning, R.A. (1975). Association of population of onychiurid Collembola with damage to sugar-beet seedlings. *Plant Pathology*, **24**, 150–4.
- Bakonyi, G. (1989). Effects of *Folsomia candida* on the microbial biomass in a grassland soil. *Biology and Fertility of Soils*, **7**, 138–41.
- Bakonyi, G., Dobolyi, C., and Thuy, L.B. (1995). ¹⁵N uptake by collembolans from bacterial and fungal food source. *Acta Zoologica Fennica*, **196**, 136–8.
- Bale, J.S. (1987). Insect cold hardiness: freezing and supercooling—an ecological perspective. *Journal of Insect Physiology*, **33**, 899–908.
- Bale, J.S. (1993). Classes of insect cold hardiness. *Functional Ecology*, **7**, 751–3.
- Bale, J.S. and Pullin, A.S. (1991). Opportunities and risks in the overwintering strategy of a wall-dwelling species of *Hypogastrura* (Collembola). *Cryo Letters*, **12**, 155–62.
- Bannon, G.A. and Engstrom, L.E. (1980). Midgut ultrastructure of an epimorphic form of *Proisotoma vesiculata* Folsom (Collembola, Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **17**, 241–50.

- Barbut, J. (1781). *The Genera Insectorum of Linnaeus exemplified by various specimens of English insects drawn from nature*. James Barbut, London.
- Bardgett, R.D., Frankland, J.C., and Whittaker, J.B. (1993a). The effects of agricultural management on the soil biota of some upland grasslands. *Agriculture, Ecosystems and Environment*, **45**, 25–45.
- Bardgett, R.D., Whittaker, J.B., and Frankland, J.C. (1993b). The effect of collembolan grazing on fungal activity in differently managed upland pastures—a microcosm study. *Biology and Fertility of Soils*, **16**, 255–62.
- Bardgett, R.D., Whittaker, J.B., and Frankland, J.C. (1993c). The diet and food preferences of *Onychiurus procamptus* (Collembola) from upland grassland soils. *Biology and Fertility of Soils*, **16**, 296–8.
- Barra, J.A. (1969a). Tégument des collemboles. Présence d'hémocytes à granules dans le liquide exuvial au cours de la mue (Insectes, Collemboles). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **269D**, 902–3.
- Barra, J.A. (1969b). Collemboles du Gabon. *Biologia Gabonica*, **5**, 189–216.
- Barra, J.A. (1970). Tégument des collemboles (Insectes). Sur un rôle inconnu des cellules tormogènes au cours du cycle de la mue. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **270D**, 3243–5.
- Barra, J.A. (1971a). Les photorécepteurs des collemboles étude ultrastructurale. 1. L'appareil dioptrique. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **117**, 322–53.
- Barra, J.A. (1971b). Les photorécepteurs des collemboles. Étude histochimique du cristallin. *Revue d'Écologie et de Biologie du Sol*, **8**, 49–53.
- Barra, J.A. (1973). Structure et régression des photorécepteurs dans le groupe *Lepidocyrtus-Pseudosinella* (Insecta, Collembola). *Annales de Spéléologie*, **28**, 167–75.
- Barra, J.A. (1975a). Le développement postembryonnaire de *Pseudosinella decipiens* et *P. impediens*. I. Études morphologique et chaetotaxique (Collembola). *Annales de Spéléologie*, **30**, 173–86.
- Barra, J.A. (1975b). Le développement postembryonnaire de *Pseudosinella decipiens* et *P. impediens*. II. Études de la croissance. *Annales de Spéléologie*, **30**, 451–61.
- Barra, J.A. (1976). Le développement postembryonnaire de *Pseudosinella decipiens* et *P. impediens* sous certaines conditions expérimentales. *Revue d'Écologie et de Biologie du Sol*, **13**, 385–97.
- Barra, J.A. (1977). La mue chez les collemboles entomobryens (Apterygota): ultrastructure et particularités. *International Journal of Insect Morphology and Embryology*, **6**, 201–19.
- Barra, J.A. (1991). Biologie et structures adaptatives des collemboles entomobryomorphes cavernicoles. *Revue d'Écologie et de Biologie du Sol*, **28**, 189–95.
- Barra, J.A. (1993). Trois nouvelles espèces de Neanuridae d'Herzégovine en région karstique (Insecta, Collembola). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **15A**, 69–78.
- Barra, J.A. (1994). Nouveaux Collembola Poduromorphes de la Province du Natal (Rép. Sud Africaine) (Insecta: Collembola). *Journal of African Zoology*, **108**, 181–9.
- Barra, J.A. and Christiansen, K. (1975). Experimental study of aggregation during the development of *Pseudosinella impediens* (Collembola, Entomobryidae). *Pedobiologia*, **15**, 343–7.
- Barra, J.A. and Poinso-Balaguer, N. (1977). Modifications ultrastructurales accompagnant l'anhydrobiose chez un Collembola: *Folsomides variabilis*. *Revue d'Écologie et de Biologie du Sol*, **14**, 189–97.
- Barra, J.A. and Poinso-Balaguer, N. (1983). Mise en évidence d'un complexe hygrophile dans les canaux transcuticulaires, chez *Folsomides angularis* en anhydrobiose. *Pedobiologia*, **25**, 279–86.
- Barra, J.A. and Poinso-Balaguer, N. (1987). Un 'terminal web' fenêtre dans le mésentéron de *Isotoma viridis* Bourlet (Collembola, Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **24**, 75–84.
- Barra, J.A., Belgnaoui, S., and Poinso-Balaguer, N. (1989). Sécheresse, froid, mêmes stratégies. Un exemple type: le collembola *Folsomides angularis*. *Bulletin d'Ecologie*, **20**, 65–6.
- Battigelli, J.P. and Marshall, V.G. (1993). Relationships between soil fauna and soil pollutants. In *Proceedings of the forest ecosystem dynamics workshop*, February 10–11 1993 (ed. V. Marshall), pp. 31–4. Forestry Canada, British Columbia Ministry of Forests.
- Bauer, R. (1993). Zür Zöologie und Phänologie granitblockbesiedelnder Collembolen. *Zoologischer Anzeiger*, **230**, 237–48.
- Bauer, R. and Christian, E. (1993). Adaptations of three springtail species to granite boulder habitats (Collembola). *Pedobiologia*, **37**, 280–90.
- Bauer, T. (1979). Die Feuchtigkeit als steuernder Faktor für das Kletterverhalten von Collembolen. *Pedobiologia*, **19**, 165–75.
- Bauer, T. (1982a). Predation by a carabid beetle specialised for catching Collembola. *Pedobiologia*, **24**, 169–79.
- Bauer, T. (1982b). Prey-capture in a ground-beetle larva. *Animal Behaviour*, **30**, 203–8.
- Bauer, T. (1985). Beetles which use a setal trap to hunt springtails: the hunting strategy and apparatus of *Leistus* (Coleoptera, Carabidae). *Pedobiologia*, **28**, 275–87.

- Bauer, T. (1990). Laufkäfer und Collembolen: Räuber-Beutebeziehungen unter Bodentieren. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, (N.F.)*, **29/30**, 29–42.
- Bauer, T. and Christian, E. (1986). Flight behaviour of springtails (Collembola) with respect to their habitat. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 177–9. University of Siena, Siena.
- Bauer, T. and Christian, E. (1987). Habitat dependent differences in the flight behaviour of Collembola. *Pedobiologia*, **30**, 233–9.
- Bauer, T. and Pfeiffer, M. (1991). Shooting springtails with a sticky rod: the flexible hunting behaviour of *Sternus comma* (Coleoptera, Staphylinidae) and the counterstrategies of its prey. *Animal Behaviour*, **41**, 819–28.
- Bauer, T. and Völlenkle, W. (1976). Hochfrequente Filmaufnahmen als Hilfsmittel bei der Analyse von Angriffs und Fluchtverhalten in einer Räuber-Beute-Beziehung unter Bodentieren (Collembolenfang visuell jagender Carabiden). *Wissenschaftliche Film* (Wien), **17**, 4–11.
- Baumbrough, B., Berch, S.M., and Marshall, V. (1992). Taxonomic survey of springtails collected from northern Vancouver Island sites. *Northwestern Environmental Journal*, **8**, 2115–17.
- Baust, J.G. (1981). Biochemical correlates to cold hardening in insects. *Cryobiology*, **18**, 186–98.
- Baweja, K.D. (1939). Studies on the soil fauna, with special reference to the recolonisation of sterilised soil. *Journal of Animal Ecology*, **8**, 120–61.
- Bedos, A. and Cassagnau, P. (1986). Facteurs genetiques et epigenetiques d'ecomorphose remanente chez *Hypogastrura boldorii* (Collembola). In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 187–91. University of Siena, Siena.
- Bedos, A. and Cassagnau, P. (1988). La réalisation de l'ecomorphose chez *Hypogastrura boldorii* (Collembola) à la tourbière du Pinet (Aude). *Revue d'Écologie et de Biologie du Sol*, **25**, 315–31.
- Bedos, A. and Deharveng, L. (1990). New species of *Superodontella* Stach (Collembola: Odontellidae) from Thailand. *Tijdschrift voor Entomologie*, **133**, 17–26.
- Bedos, A. and Deharveng, L. (1991). *Cephalachorutes* gen. n., a new genus of tropical Neanuridae (Collembola). *Tijdschrift voor Entomologie*, **134**, 145–53.
- Bedos, A. and Deharveng, L. (1994). The *Isotomiella* of Thailand (Collembola: Isotomidae), with description of five new species. *Entomologica Scandinavica*, **25**, 451–60.
- Beeby, A. (1991). Toxic metal uptake and essential metal regulation in terrestrial invertebrates: a review. In *Metal ecotoxicology* (ed. M.C. Newman and A.W. McIntosh), pp. 65–89. Lewis, Michigan.
- Behan-Pelletier, V.M. (1993). Diversity of soil arthropods in Canada: systematic and ecological problems. *Memoirs of the Entomological Society of Canada*, **165**, 11–50.
- Belgnaoui, S. and Barra, J.A. (1988a). Cytochrome oxidase activity in the anhydrobiotic Collembola *Folsomides angularis* (Insecta, Apterygota). *Pedobiologia*, **32**, 283–91.
- Belgnaoui, S. and Barra, J.A. (1988b). Anhydrobiosis in the Collembola *Folsomides angularis*. Cytochemical investigations of glycogen status and glycogen phosphorylase activity. *Biological Structures and Morphogenesis*, **1**, 147–53.
- Belgnaoui, S. and Barra, J.A. (1989). Water loss and survival in the anhydrobiotic Collembola *Folsomides angularis* (Insecta). *Revue d'Écologie et de Biologie du Sol*, **26**, 123–32.
- Bellinger, P.F. (1962). A dimorphic species of *Actaetes* (Collembola). *Journal of the New York Entomological Society*, **70**, 88–91.
- Bellinger, P.F. (1985a). A new Family of Collembola (Arthropoda, Tracheata). *Caribbean Journal of Science*, **21**, 117–23.
- Bellinger, P.F. (1985b). The identity of H.G. Scott's Collembola in the Academy of Natural Sciences, Philadelphia, PA. *Entomological News*, **96**, 78–82.
- Bellinger, P.F. and Christiansen, K.A. (1974). The cavernicolous fauna of Hawaiian lava tubes. 5. Collembola. *Pacific Insects*, **16**, 31–40.
- Bellinger, P.F. and Christiansen, K. (1989). Biogeography of the Collembola of Hawaii. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 121–6. University of Siena, Siena.
- Bengtsson, G. and Rundgren, S. (1983). Respiration and growth of a fungus *Mortierella isabellina* in response to grazing by *Onychiurus armatus* (Collembola). *Soil Biology and Biochemistry*, **15**, 469–73.
- Bengtsson, G. and Rundgren, S. (1988). The Gusum case: a brass mill and the distribution of soil Collembola. *Canadian Journal of Zoology*, **66**, 1518–26.
- Bengtsson, G., Gunnarsson, T., and Rundgren, S. (1983). Growth changes caused by metal uptake in a population of *Onychiurus armatus* (Collembola) feeding on metal polluted fungi. *Oikos*, **40**, 216–25.
- Bengtsson, G., Gunnarsson, T., and Rundgren, S. (1985a). Influence of metals on reproduction, mortality and growth in *Onychiurus armatus* (Collembola). *Journal of Applied Ecology*, **22**, 967–78.
- Bengtsson, G., Ohlsson, L., and Rundgren, S. (1985b). Influence of fungi on growth and survival of *Onychiurus armatus* (Collembola) in a metal polluted soil. *Oecologia*, **68**, 63–8.

- Bengtsson, G., Erlandsson, A., and Rundgren, S. (1988). Fungal odour attracts soil Collembola. *Soil Biology and Biochemistry*, **20**, 25–30.
- Bengtsson, G., Hedlund, K., and Rundgren, S. (1991). Selective odour perception in the soil Collembola *Onychiurus armatus*. *Journal of Chemical Ecology*, **17**, 2113–25.
- Bengtsson, G., Hedlund, K., and Rundgren, S. (1993). Patchiness and compensatory growth in a fungus-Collembola system. *Oecologia*, **93**, 296–302.
- Bengtsson, G., Rundgren, S., and Sjögren, M. (1994a). Modelling dispersal distances in a soil gradient: the influence of metal resistance, competition and experience. *Oikos*, **71**, 13–23.
- Bengtsson, G., Hedlund, K., and Rundgren, S. (1994b). Food- and density-dependent dispersal: evidence from a soil collembolan. *Journal of Animal Ecology*, **63**, 513–20.
- Bengtsson, J. (1994). Temporal predictability in forest soil communities. *Journal of Animal Ecology*, **63**, 653–65.
- Berbiere, P. and Segers, H. (1991). Collembola of the Zonien Forest (Province Brabant, Belgium). *Bulletin et Annales de la Société Royale Entomologique de Belgique*, **127**, 81–5.
- Berbiere, P., Maelfait, J.P., and Mertens, J. (1989). Evaluation of some sampling methods used to study Collembola (Insecta, Apterygota) in a pasture. *Revue d'Écologie et de Biologie du Sol*, **26**, 305–20.
- Bernard, E.C. and Snider, R.J. (1994). *Cryptopygus bipunctatus* (Collembola: Isotomidae) in North America, and *C. posteroalatus* n. comb. *Great Lakes Entomologist*, **27**, 149–56.
- Bertolani, R., Sabatini, M.A., and Mola, L. (1989). Effects of change in tillage practices on Collembola populations. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 291–297. University of Siena, Siena.
- Beruete, E., Arbea, J.I., and Jordana, R. (1994). Contribución al conocimiento de las especies de *Onychiurus* del grupo *O. minutus* (Collembola, Onychiuridae). *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **24**, 19–37.
- Best, G.R., Nabholz, J.V., Ojasti, J., and Crossley, D.A. (1978). Response of microarthropod populations to naphthalene in three contrasting habitats. *Pedobiologia*, **18**, 189–201.
- Betsch, J.M. (1965a). Collembolles Symphypléones de la Jamaïque (Première note). *Revue d'Écologie et de Biologie du Sol*, **2**, 439–51.
- Betsch, J.M. (1965b). Remarque sur le développement de l'orifice génital et de l'appendice anal de *Sphyrotheca bellingeri* n.sp. *Revue d'Écologie et de Biologie du Sol*, **2**, 525–33.
- Betsch, J.M. (1967). Développement des caractères sexuels secondaires chez *Bovicornia greensladei* Massoud et Delamare Deboutteville. *Revue d'Écologie et de Biologie du Sol*, **4**, 299–311.
- Betsch, J.M. (1969). Contribution à l'étude des Sminthuridinae (Collembolles, Symphypléones) un genre nouveau d'Australie: *Pygicornides*. *Revue d'Écologie et de Biologie du Sol*, **6**, 349–55.
- Betsch, J.M. (1970). Étude des Collembolles de Madagascar. I. Description d'un nouveau genre de Symphypléones: *Zebulonia*. *Revue d'Écologie et de Biologie du Sol*, **7**, 51–70.
- Betsch, J.M. (1971). Étude préliminaire de la répartition des *Temeritas* Delamare et Massoud (Collembolles Symphypléones à Madagascar). *Revue d'Écologie et de Biologie du Sol*, **8**, 167–72.
- Betsch, J.M. (1974a). Étude des Collembolles de Madagascar. II. Principaux cadres génériques des Symphypléones de l'étage montagnard. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 3, Zoologie*, **147**, 529–69.
- Betsch, J.M. (1974b). Étude des Collembolles de Madagascar. III. Un nouveau genre de Bourletiellidae (Symphypleona): *Massoudia griveaudi* n.g., n.sp. *Revue d'Écologie et de Biologie du Sol*, **11**, 561–7.
- Betsch, J.M. (1974c). Contribution à l'étude de la reproduction chez les Bourletiellinae (Collembolles, Symphypléones). *Pedobiologia*, **14**, 179–81.
- Betsch, J.M. (1975a). Étude des Collembolles de Madagascar. IV. Deux nouveaux genres de Symphypléones à dimorphisme sexuel important: *Parabourletiella* et *Richardsitas*. *Revue d'Écologie et de Biologie du Sol*, **12**, 477–85.
- Betsch, J.M. (1975b). Existence de deux phases juvéniles chez les Collembolles Symphypléones. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **281D**, 1601–3.
- Betsch, J.M. (1977a). Étude des Collembolles de Madagascar. V. Sur deux Symphypléones de la forêt sèche en secteur bioclimatique subaride. *Bulletin de la Société Entomologique de France*, **82**, 119–25.
- Betsch, J.M. (1977b). Évolution des caractères génériques au cours de la période immature des Collembolles Symphypléones. *Revue d'Écologie et de Biologie du Sol*, **14**, 181–8.
- Betsch, J.M. (1977c). Mise au point sur la systématique des Collembolles Symphypléones. *Revue d'Écologie et de Biologie du Sol*, **14**, 211–15.
- Betsch, J.M. (1977d). Collembolles Symphypléones de la Mongolie (Collembola). *Annales Historico-Naturales Musei nationalis Hungarici*, **69**, 59–88.
- Betsch, J.M. (1980). Éléments pour une monographie des Collembolles Symphypléones (Hexapodes, Aptérygotes). *Mémoires du Muséum National d'Histoire Naturelle*, **116A**, 1–227.

- Betsch, J.M. (1991). Effets de la privation des apports annuels de litière sur les Collembolles Symphypléones épigés d'une forêt sur rendzine. *Revue d'Écologie et de Biologie du Sol*, **28**, 41–9.
- Betsch, J.M. and Betsch-Pinot, M.C. (1984). Contribution à l'étude des *Sminthurus* (Collembola, Symphypleona). *Annales de la Société Royale Zoologique de Belgique*, **114**, 71–81.
- Betsch, J.M. and Brefeld, G. (1991). A proposal for a standard system of chaetotaxic nomenclature in the Symphypleona (Insecta: Collembola). In *Advances in Management and Conservation of Soil Fauna* (ed. G.K. Veeresh, D. Rajagopal and C.A. Viraktamath), pp. 31–8. Oxford and IBH, New Delhi.
- Betsch, J.M. and Cancela da Fonseca, J.P. (1995). Changes in edaphic factors and microarthropod communities after clearing and burning in a tropical rain forest in French Guyana. *Acta Zoologica Fennica*, **196**, 142–5.
- Betsch, J.M. and Cassagnau, P. (1966). Présence de caractères sexuels secondaires chez les mâles d'*Arrhopalites* (Collembolles). *Revue d'Écologie et de Biologie du Sol*, **3**, 123–8.
- Betsch, J.M. and Lasebikan, B.A. (1979). Collembolles du Nigeria. I. *Stenognathriopes*, un nouveau genre de Symphypléones. *Bulletin de la Société Entomologique de France*, **84**, 165–70.
- Betsch, J.M. and Massoud, Z. (1970). Étude sur les Insectes Collembolles. I. Systématique, ultrastructure externe et écologie du genre *Jeannenotia* Stach 1956 (Symphypléones, Sminthuridae n.comb.). Description de deux Collembolles nouveaux (*Proisotoma* et *Sminthurides*). *Revue d'Écologie et de Biologie du Sol*, **7**, 153–225.
- Betsch, J.M. and Massoud, Z. (1972). Collembolles Symphypléones d'Australie: *Bourletides*, n.g. et *Pygicormides*. *Annales de la Société Entomologique de France*, N.S., **8**, 225–37.
- Betsch, J.M. and Massoud, Z. (1973). Découverte de la femelle de *Microfalcula delamarei* (Collembolles, Microfalculinae). *Nouvelle Revue d'Entomologie*, **3**, 5–7.
- Betsch, J.M. and Vannier, G. (1977). Caractérisation des deux phases juvéniles d'*Allacma fusca* (Collembola, Symphypleona) par leur morphologie et leur écophysologie. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **15**, 124–41.
- Betsch, J.M. and Waller, A. (1989). L'armement en trichobothries des Collembolles Symphypléones: recherches de schémas chaetotaxiques. In *Third International Seminar on Apterygota*, (ed. R. Dallai), pp. 15–31. University of Siena, Siena.
- Betsch, J.M. and Waller, A. (1991). Collembolles Symphypléones de Guyane. I. Un nouveau genre de Sminthuridae. *Revue d'Écologie et de Biologie du Sol*, **28**, 229–35.
- Betsch, J.M. and Waller, A. (1994). Chaetotaxic nomenclature of the head, thorax and abdomen in Symphypleona (Insecta, Collembola). *Acta Zoologica Fennica*, **195**, 5–12.
- Betsch, J.M. and Weiner, W.M. (1987). Le genre *Bothriovulsus* Richards, 1968 (Collembola, Symphypleona). Intérêt phylétique et place au sein des Dicyrtomidae. In *Soil fauna and soil fertility* (ed. B.R. Striganova), pp. 622–6. Nauka, Moscow.
- Betsch, J.M., Betsch-Pinot, M.C., and Vannier, G. (1980). La conquête du milieu aérien par les Insectes: le groupe pionnier des Collembolles Symphypléones résultante de multiples adaptations biologiques. In *Recherches d'écologie théorétiques. Les stratégies adaptatives* (ed. R. Barbault, P. Blandin, and J.A. Meyer), pp. 77–88. Maloine, Paris.
- Betsch, J.M., Thibaud, J.M., and Najt, J. (1990). Progres recents apportées dans la taxinomie des Insectes Collembolles en particulier par l'analyse des homologues morphologiques. *Bulletin de la Société Zoologique de France*, **115**, 165–80.
- Betsch-Pinot, M.C. (1974a). Développement post-embryonnaire de la plaque génitale de la femelle de *Proisotoma minuta* (Tullberg, 1871) (Collembolles, Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **11**, 2113–18.
- Betsch-Pinot, M.C. (1974b). Développement post-embryonnaire de la plaque génitale du mâle de *Proisotoma minuta* (Collembola, Isotomidae). *Pedobiologia*, **14**, 269–72.
- Betsch-Pinot, M.C. (1976). Le comportement reproducteur de *Sminthurus viridis* (L.) (Collembola, Symphypleona). *Zeitschrift für Tierpsychologie*, **40**, 427–39.
- Betsch-Pinot, M.C. (1977). Les parades sexuelles primitives chez les Collembolles Symphypléones. *Revue d'Écologie et de Biologie du Sol*, **14**, 115–19.
- Betts, M.M. (1955). Food of titmice in oak woodland. *Journal of Animal Ecology*, **24**, 282–323.
- Bilinski, S. (1976). Ultrastructural study on the vitellogenesis of *Tetrodontophora bielanensis* (Waga) (Collembola). *Cell and Tissue Research*, **168**, 399–410.
- Bilinski, S.M. (1993). Structure of ovaries and oogenesis in entognathans (Apterygota). *International Journal of Insect Morphology and Embryology*, **22**, 255–69.
- Blackith, R.E. (1974). The ecology of Collembola in Irish blanket bogs. *Proceedings of the Royal Irish Academy*, **74B**, 203–26.
- Blackith, R.E. and Blackith, R.E. (1975). Zoogeographical and ecological determinants of collembolan distribution. *Proceedings of the Royal Irish Academy*, **75B**, 345–68.

- Blackith, R.E. and Disney, R.H.L. (1988). Passive dispersal during moulting in tropical Collembola. *Malayan Nature Journal*, **41**, 529–31.
- Blancquaert, J.P. (1981). Mating behaviour in some Sminthurididae (Collembola) with reference to the systematics of Symphypleona. *Pedobiologia*, **22**, 1–4.
- Blancquaert, J.P. and Mertens, J. (1977). Mating behaviour in *Sphaeridia pumilis* (Collembola). *Pedobiologia*, **17**, 343–9.
- Blancquaert, J.P. and Mertens, J. (1979). Postembryonal development in *Megalothorax minimus* (Willem, 1900) (Collembola). *Revue d'Écologie et de Biologie du Sol*, **16**, 125–30.
- Blancquaert, J.P., Coessens, R., and Mertens, J. (1981a). Life history of some Symphypleona (Collembola) under experimental conditions. I. Embryological development and diapause. *Revue d'Écologie et de Biologie du Sol*, **18**, 115–26.
- Blancquaert, J.P., Coessens, R., and Mertens, J. (1981b). Life history of some Symphypleona (Collembola) under experimental conditions. II. Post-embryonal development and reproduction. *Revue d'Écologie et de Biologie du Sol*, **18**, 373–90.
- Blancquaert, J.P., Mertens, J., and Coessens, R. (1982). Annual cycle of populations of *Sphaeridia pumilis* (Collembola). *Revue d'Écologie et de Biologie du Sol*, **19**, 605–11.
- Block, W. (1979a). Cold tolerance of micro-arthropods from Alaskan taiga. *Ecological Entomology*, **4**, 103–10.
- Block, W. (1979b). Oxygen consumption of the Antarctic springtail *Parisotoma octooculata* (Willem) (Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **16**, 227–33.
- Block, W. (1979c). Terrestrial invertebrates. In *Elephant Island Antarctic Expedition, Appendix E* (ed. C. Furse), pp. 226–9. Anthony Nelson, Shrewsbury.
- Block, W. (1980). Aspects of the ecology of Antarctic soil fauna. In *Soil biology as related to land use practices* (ed. D.L. Dindal), pp. 741–57. Environmental Protection Agency, Washington, D.C.
- Block, W. (1981). Low temperature effects on micro-arthropods. *Journal of Thermal Biology*, **6**, 2115–18.
- Block, W. (1982a). The Signy Island terrestrial reference sites. XIV. Population studies on the Collembola. *British Antarctic Survey Bulletin*, **55**, 33–49.
- Block, W. (1982b). Supercooling points of insects and mites on the Antarctic Peninsula. *Ecological Entomology*, **7**, 1–8.
- Block, W. (1982c). Cold hardiness in invertebrate poikilotherms. *Comparative Biochemistry and Physiology*, **73A**, 581–93.
- Block, W. (1983). Heterogeneous ice nucleation in super-cooled micro-arthropods. *Cryo-Letters*, **4**, 155–62.
- Block, W. (1984a). Terrestrial microbiology, invertebrates and ecosystems. In *Antarctic ecology* Volume 1 (ed. R.M. Laws), pp. 163–236. Academic Press, London.
- Block, W. (1984b). A comparative study of invertebrate supercooling at Signy Island, maritime Antarctic. *British Antarctic Survey Bulletin*, **64**, 67–76.
- Block, W. (1985a). Arthropod interactions in an Antarctic terrestrial community. In *Nutrient cycling and food webs in the Antarctic* (ed. W.R. Siegfried, P. Condy, and R.M. Laws), pp. 6114–19. Springer-Verlag, Berlin.
- Block, W. (1985b). Ecological and physiological studies of terrestrial arthropods in the Ross Dependency 1984–85. *British Antarctic Survey Bulletin*, **68**, 115–22.
- Block, W. (1987). Ecophysiology of terrestrial arthropods. *Comité National Français des Recherches Antarctiques*, **58**, 99–106.
- Block, W. (1990). Cold tolerance of insects and other arthropods. *Philosophical Transactions of the Royal Society of London*, **326B**, 613–33.
- Block, W. (1991). To freeze or not to freeze? Invertebrate survival of sub-zero temperatures. *Functional Ecology*, **5**, 284–90.
- Block, W. (1992). *An annotated bibliography of Antarctic invertebrates (terrestrial and freshwater)*. British Antarctic Survey, Natural Environment Research Council, Cambridge.
- Block, W. (1994). Differential scanning calorimetry in ecophysiological research. *Acta Oecologia*, **15**, 13–22.
- Block, W. and Sømme, L. (1982). Studies of arthropod cold hardiness. *British Antarctic Survey Bulletin*, **53**, 265–6.
- Block, W. and Tilbrook, P.J. (1975). Respiration studies on the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos*, **26**, 15–25.
- Block, W. and Tilbrook, P.J. (1977). Effects of long-term storage on the oxygen uptake of *Cryptopygus antarcticus* (Collembola). *Oikos*, **29**, 284–9.
- Block, W. and Tilbrook, P.J. (1978). Oxygen uptake by *Cryptopygus antarcticus* (Collembola) at South Georgia. *Oikos*, **30**, 61–7.
- Block, W. and Zettel, J. (1980). Cold hardiness of some alpine Collembola. *Ecological Entomology*, **5**, 1–9.

- Block, W., Young, S.R., Conradi-Larsen, E.M., and Sømme, L. (1978). Cold tolerance of two Antarctic terrestrial arthropods. *Experientia*, **34**, 1166–7.
- Block, W., Harrison, P.M., and Vannier, G. (1990). A comparative study of patterns of water loss from two Antarctic springtails (Insecta, Collembola). *Journal of Insect Physiology*, **36**, 181–7.
- Block, W., Webb, N.R., Coulson, S., Hodgkinson, I.D., and Worland, M.R. (1994). Thermal adaptation in the Arctic collembolan *Onychiurus arcticus* (Tullberg). *Journal of Insect Physiology*, **40**, 715–22.
- Blottner, D. and Eisenbeis, G. (1984). Ultrastructure of long tibiotarsal spatula-hairs in *Tomocerus flavescens* (Collembola: Tomoceridae). *Annales de la Société Royale Zoologique de Belgique*, **114**, 51–7.
- Bödvarsson, H. (1959). Studien über die Variation einiger systematischen Charaktere bei *Onychiurus armatus* (Tullberg, 1869) (Collembola). *Opuscula Entomologica*, **24**, 225–45.
- Bödvarsson, H. (1960a). One new genus and three new species of Collembola from Alaska. *Opuscula Entomologica*, **25**, 43–51.
- Bödvarsson, H. (1960b). Beitrag zur Kenntnis der Collembolenfauna der Färöerinseln. *Opuscula Entomologica*, **25**, 173–8.
- Bödvarsson, H. (1961). Beitrag zur Kenntnis der südschwedischen bodenlebenden Collembolen. *Opuscula Entomologica*, **26**, 178–98.
- Bödvarsson, H. (1966). Collembola from southeastern Iceland including material from the margin of a receding glacier. *Opuscula Entomologica*, **31**, 221–53.
- Bödvarsson, H. (1967). Icelandic Collembola. Material from the Westman Islands and from Hornafjörður, southeastern Iceland. *Opuscula Entomologica*, **32**, 255–70.
- Bödvarsson, H. (1970a). Studies of *Onychiurus armatus* (Tullberg) and *Folsomia quadrioculata* (Tullberg) (Collembola). *Opuscula Entomologica, Supplementum*, **36**, 1–182.
- Bödvarsson, H. (1970b). Alimentary studies of seven common soil-inhabiting Collembola of southern Sweden. *Entomologica Scandinavica*, **1**, 74–80.
- Bödvarsson, H. (1973). Contributions to the knowledge of Swedish forest Collembola. Institute of Forest Zoology, Royal College of Forestry, Stockholm. Research Works Number 13, pp. 1–43.
- Boerner, R.E.J. and Harris, K.K. (1991). Effects of Collembola (Arthropoda) and relative germination date of competition between mycorrhizal *Panicum virgatum* (Poaceae) and non-mycorrhizal *Brassica nigra* (Brassicaceae). *Plant and Soil*, **136**, 121–9.
- Böhle, W. (1991). Die Collembolenfauna des Vogelbergs. *Hessische Faunistische Briefe*, **11** (3), 35–56.
- Bolger, T. (1984). Applications of binary discriminant analysis in the study of microarthropod communities. *Journal of Life Sciences of the Royal Dublin Society*, **5**, 51–5.
- Bolger, T. (1985). The rate of disappearance of *Salix* litter on cutaway bog and the microarthropods associated with it. *Pedobiologia*, **28**, 145–53.
- Bolger, T. (1986). The Collembola of Ireland: a checklist and bibliography. *Proceedings of the Royal Irish Academy*, **86B**, 183–218.
- Bolger, T. and Curry, J.P. (1980). Effects of cattle slurry on soil arthropods in grassland. *Pedobiologia*, **20**, 246–53.
- Bonnet, L., Cassagnau, P., and De Izarra, D.C. (1972). Étude écologique des Collembolles muscicoles du Sidobre (Tarn). III. Répartition des espèces en fonction des biotopes. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **108**, 263–79.
- Bonnet, L., Bougeois, A., and Cassagnau, P. (1973). Valeur et limites des critères chétotaxiques chez les Collembolles Hypogastruridae: analyse biométrique des soies axiales chez les *Ceratophysella*. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **109**, 35–51.
- Bonnet, L., Cassagnau, P., and Travé, J. (1975). L'écologie des arthropodes muscicoles à la lumière de l'analyse des correspondances: Collembolles et Oribates du Sidobre (Tarn, France). *Oecologia*, **21**, 359–73.
- Bonnet, L., Cassagnau, P., and Deharveng, L. (1976). Un exemple de rupture de l'équilibre biocénétique par déboisement: les peuplements de Collembolles édaphiques du Piau d'Engaly (Hautes-Pyrénées). *Revue d'Écologie et de Biologie du Sol*, **13**, 337–51.
- Bonnet, L., Cassagnau, P., Deharveng, L. (1977). Influence de déboisement et du rebioisement sur les biocénoses de Collembolles dans quelques sols pyrénéens. *Bulletin d'Écologie*, **8**, 321–32.
- Bonnet, L., Cassagnau, P., and Deharveng, L. (1979). Recherche d'une méthodologie dans l'analyse de la rupture des équilibres biocénétiques: applications aux Collembolles édaphiques des Pyrénées. *Revue d'Écologie et de Biologie du Sol*, **16**, 373–401.
- Boore, J.L., Collins, T.M., Stanton, D., Daehler, L.L., and Brown, W.M. (1995). Deducing the pattern of arthropod phylogeny from mitochondrial DNA rearrangements. *Nature*, **376**, 163–5.
- Booth, R.G. (1983). Effects of plaster-charcoal substrate variation on the growth and fecundity of *Folsomia candida* (Collembola, Isotomidae). *Pedobiologia*, **25**, 187–95.

- Booth, R.G. and Anderson, J.M. (1979). The influence of fungal food quality on the growth and fertility of *Folsomia candida* (Collembola: Isotomidae). *Oecologia*, **38**, 317–23.
- Booth, R.G. and Usher, M.B. (1984). Arthropod communities in maritime Antarctic moss-turf habitat: effects of the physical and chemical environment. *Journal of Animal Ecology*, **53**, 879–93.
- Booth, R.G. and Usher, M.B. (1985). Relationships between Collembola and their environment in a maritime Antarctic moss-turf habitat. In *Ecological interactions in soil: plants, microbes and animals* (ed. A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher), pp. 279–284. Blackwell, Oxford.
- Borio, R., Chiocchini, S., Cicioni, R., Esposti, P.D., Rongoni, A., Sabatini, P., Scampolì, P., Antonini, A., and Salvadori, P. (1991). Uptake of radiocesium by mushrooms. *Science of the Total Environment*, **106**, 183–90.
- Borkott, H. and Insam, H. (1990). Symbiosis with bacteria enhances the use of chitin by the springtail *Folsomia candida* (Collembola). *Biology and Fertility of Soils*, **9**, 126–9.
- Börner, C. (1901a). Vorläufige Mitteilungen über einige neue Aphorurinen und zur Systematik der Collembola. *Zoologischer Anzeiger*, **24**, 1–15.
- Börner, C. (1901b). Ueber ein neues Achorutiden genus *Willemia* sowie 4 weitere neue Collembolen formen derselben Familie. *Zoologischer Anzeiger*, **24**, 422–33.
- Börner, C. (1906a). Das System der Collembolen, nebst beschreibungen neuer Collembolen des Hamburger Naturhistorischen Museums. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg*, **23**, 147–88.
- Börner, C. (1906b). Collembola Symphypleona Fam. Neelidae. *Genera Insectorum*, **1**, 1–5.
- Börner, C. (1913). Die Familien der Collembolen. *Zoologischer Anzeiger*, **41**, 315–22.
- Bourgeois, A. (1973). Polymorphisme et épitoquie chez *Ceratophysella tuberculata* (Collembola, Hypogastruridae). *Revue d'Écologie et de Biologie du Sol*, **10**, 589–601.
- Bourgeois, A. (1974). Nouveaux cas d'épitoquie chez les Collemboles Hypogastruridae. *Pedobiologia*, **14**, 191–5.
- Bourgeois, A. (1982). L'épitoquie chez les Collemboles Hypogastruridae: *Ceratophysella bengtssoni*. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **117**, 196–202.
- Bourlet, A. (1839). Mémoires sur les Podures. *Mémoires de la Société Royale des Sciences de l'Agriculture et des Arts de Lille*, **1**, 377–417.
- Bourlet, A. (1843). Memoire sur les Podurelles. *Mémoires de la Société Royale de Douai*, 1–78.
- Bouthier, A. and Thibaud, J.M. (1974). Recherches sur la pigmentation ommochromique des Insectes Collembola en relation avec leur biotope. *Pedobiologia*, **14**, 103–5.
- Bowden, J., Haines, I.H., and Mercer, D. (1976). Climbing Collembola. *Pedobiologia*, **16**, 298–312.
- Bowler, P.J. (1994). Are the Arthropoda a natural group? An episode in the history of evolutionary biology. *Journal of the History of Biology*, **27**, 177–213.
- Brackenbury, J. (1990). A novel method of self-righting in the springtail *Sminthurus viridis* (Insecta, Collembola). *Journal of Zoology*, **222**, 1117–19.
- Brackenbury, J. and Hunt, H. (1993). Jumping in springtails: mechanism and dynamics. *Journal of Zoology*, **229**, 217–36.
- Brauner, U. (1981). Vergleichende anatomische Untersuchungen zum Nervensystem der Collembolen (Hexapoda, Apterygota). *Zoologische Jahrbücher für Anatomie*, **105**, 259–90.
- Bretfeld, G. (1963). Zur Anatomie und Embryologie der Rumpfmuskulatur und die abdominalen Anhangs der Collembolen. *Zoologische Jahrbücher für Anatomie*, **80**, 309–84.
- Bretfeld, G. (1970). Grundzüge des Paarungsverhaltens europäischer Bourlettiellini (Collembola, Sminthuridae) und daraus abgeleitete taxonomische-nomenklatorische Folgerungen. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **8**, 259–73.
- Bretfeld, G. (1971). Das Paarungsverhalten europäischer Bourlettiellini (Sminthuridae). *Revue d'Écologie et de Biologie du Sol*, **8**, 145–53.
- Bretfeld, G. (1973). *Heterosminthurus bilineatus* (Collembola). Balz und Spermaübertragung. *Encyclopaedia Cinematographica*, **E2015**, 1–10.
- Bretfeld, G. (1974). *Heterosminthurus bilineatus* (Collembola). Balz und Spermaübertragung (Film E2015, Encyclopaedia Cinematographica, Göttingen). *Pedobiologia*, **14**, 178.
- Bretfeld, G. (1976a). *Heterosminthurus bilineatus* (Collembola). Balz und Spermaübertragung. *Encyclopaedia Cinematographica*, **E2248**, 1–8.
- Bretfeld, G. (1976b). *Heterosminthurus chaetocephalus* (Collembola). Balz und Spermaübertragung. *Encyclopaedia Cinematographica*, **E2252**, 1–10.
- Bretfeld, G. (1977). Der Zyklus von Häutung, Paarung und Eiablage bei den Weibchen von *Heterosminthurus insignis* (Reuter, 1876) (Collembola, Symphypleona). *Revue d'Écologie et de Biologie du Sol*, **14**, 1–13.

- Bretfeld, G. (1986a). A new chaetotaxic character in some *Heterosminthurus* species (Insecta, Collembola, Symphypleona). In *Second International Seminar on Apterygota*, (ed. R. Dallai), pp. 19–22. University of Siena, Siena.
- Bretfeld, G. (1986b). Phylogenetic systematics of the higher taxa of Symphypleona Börner, 1901 (Insecta, Entognatha, Collembola). In *Second International Seminar on Apterygota*, (ed. R. Dallai), pp. 307–11. University of Siena, Siena.
- Bretfeld, G. (1988). Zwei neue Farbformen von *Heterosminthurus insignis* (Reuter, 1876) und Unterscheidungsmerkmale zu *Heterosminthurus novemlineatus* (Tullberg, 1871) (Insecta, Collembola, Symphypleona). *Abhandlungen und Berichte des Naturkundemuseums Gorlitz*, **62** (5), 1–8.
- Bretfeld, G. (1989a). The present state of distribution maps of some species of European Collembola Symphypleona (Insecta, Entognatha). A demonstration. In *Third International Seminar on Apterygota* (ed. R. Dallai), p. 119. University of Siena, Siena.
- Bretfeld, G. (1989b). Chorologie und Ökologie von sieben europäischen Arten der Collembola Symphypleona (Insecta, Entognatha). *Zoologische Jahrbücher für Systematik*, **116**, 293–327.
- Bretfeld, G. (1990). Chaetotaxy of four species of the genera *Heterosminthurus*, *Bourletiella*, *Deuterosminthurus*, and *Prorastriopes* (Insecta, Collembola, Symphypleona). *Zoologische Jahrbücher für Systematik*, **117**, 441–89.
- Bretfeld, G. (1991). A preparation method for Symphypleona (Insecta, Collembola) with some comments on the history of this method. *Revue d'Écologie et de Biologie du Sol*, **28**, 2117–19.
- Bretfeld, G. (1992a). Description of old and new European taxa of the genus *Fasciosminthurus* Gisin, 1960 n.comb. (Collembola, Symphypleona) mainly based on chaetotaxy. *Mitteilungen aus dem Zoologischen Museum in Kiel, Supplementum*, **4**, 7–36.
- Bretfeld, G. (1992b). Generic division of *Prorastriopes* Betsch, 1977 with description of *Cyprania* n.g. from Cyprus (Collembola, Symphypleona). *Mitteilungen aus dem Zoologischen Museum in Kiel, Supplementum*, **4**, 37–60.
- Bretfeld, G. (1994a). *Sturmius epiphytus* n.gen. n.spec. from Columbia, a taxon of the Symphypleona (Insecta, Collembola) with an unexpected character combination: description and position in non-Linnean and Linnean classifications in the Symphypleona. *Journal of Zoological Systematic and Evolutionary Research*, **32**, 264–81.
- Bretfeld, G. (1994b). The chaetotaxy of the small abdomen of the Symphypleona (Insecta, Collembola) and its phylogenetic interpretation. *Acta Zoologica Fennica*, **195**, 113–17.
- Bretfeld, G. (1994c). Two new species of the genus *Bourletiella* Banks 1899, s.str. from Portugal and Spain. *Senckenbergiana biologica*, **74**, 147–52.
- Bretfeld, G. and Gauer, U. (1994). Diagnostic description of the males of new *Sphaeridia* species (Insecta, Collembola) from South America. *Andrias*, **13**, 113–36.
- Bretschko, G. and Christian, E. (1989). Collembola in the bed sediments of an alpine gravel stream (RITRODAT-Lunz study area, Austria). *Internationale Revue der Gesamten Hydrobiologie*, **74**, 491–8.
- Broady, P.A. (1979). Feeding studies on the collembolan *Cryptopygus antarcticus* Willem at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, **48**, 37–46.
- Brook, G. (1883). Notes on some little-known Collembola, and on the British species of the genus *Tomocerus*. *Journal of the Linnean Society of London (Zoology)*, **17**, 19–25.
- Brook, G. (1884). A revision of the genus *Entomobrya*, Rond. (*Degeeria*, Nic.). *Journal of the Linnean Society of London (Zoology)*, **17**, 270–83.
- Brown, E.B. (1954). Springtail damage to tomatoes. *Plant Pathology*, **3**, 87–8.
- Brown, J.M. (1921). The swarming of Collembola. *Naturalist (Hull)*, 129–30.
- Broza, M., Poliakov, D., Weber, S. and Izhaki, I. (1993). Soil microarthropods on postfire pine forest on Mount Carmel, Israel. *Water Science and Technology*, **27**, 533–8.
- Brückmann, A. and Wolters, V. (1994). Microbial immobilization and recycling of ^{137}Cs in the organic layers of forest ecosystems: relationship to environmental conditions, humification and invertebrate activity. *Science of the Total Environment*, **157**, 249–56.
- Bruckmoser, P. (1965). Embryologische Untersuchungen über den Kopfbau der Collembole *Orchesella villosa* L. *Zoologische Jahrbücher für Anatomie*, **82**, 299–364.
- Brummer-Korvenkontio, M. and Brummer-Korvenkontio, L. (1980). Springtails (Collembola) on and in snow. *Memoirs Societas pro Fauna et Flora Fennica*, **56**, 91–4.
- Brummer-Korvenkontio, M. and Saure, L. (1969). Further observations on the chromosome relation in female Collembola. *Aquilo Zoologica*, **9**, 50–4.
- Büchs, W. (1994). Effects of different input of pesticides and fertilizers on the abundance of arthropods in a sugar beet crop: an example for a long-term risk assessment in the field. In *Ecotoxicology of soil organisms* (ed. M.H. Donker, H. Eijssackers, and F. Heimbach), pp. 303–21. Lewis, Boca Raton.

- Budaeva, L.I. (1993). Peculiarities of surface dwelling collembolan communities (Collembola) in Khakasia steppe. *Zoologicheskyy Zhurnal*, **72**, 45–52.
- Bulavintsev, V.I. and Babenko, A.B. (1989). Springtails (Collembola, Apterygota) in the polar desert of the Bolshevik Island (Severnaya Zemlya). *Zoologicheskyy Zhurnal*, **68**, 146–9.
- Burn, A.J. (1981). Feeding and growth in the Antarctic collembolan *Cryptopygus antarcticus*. *Oikos*, **36**, 59–64.
- Burn, A.J. (1982). Effects of temperature on the feeding activity of *Cryptopygus antarcticus*. *Comité National Français des Recherches Antarctiques*, **51**, 209–17.
- Burn, A.J. (1984a). Life cycle strategies in two Antarctic Collembola. *Oecologia*, **64**, 223–9.
- Burn, A.J. (1984b). Energy partitioning in the Antarctic collembolan *Cryptopygus antarcticus*. *Ecological Entomology*, **9**, 11–21.
- Butcher, J.W., Kirknel, E., and Zabik, M. (1969). Conversion of DDT to DDE by *Folsomia candida* (Willem). *Revue d'Écologie et de Biologie du Sol*, **6**, 291–8.
- Butcher, J.W., Snider, R., and Snider, R.J. (1971). Bioecology of edaphic Collembola and Acarina. *Annual Review of Entomology*, **16**, 249–88.
- Calandrino, F. (1987). New colour pattern and morphological variation found in *Tomocerus flavescens* (Collembola, Entomobryidae). *Entomological News*, **98**, 180–2.
- Calow, P. (1989). Ecotoxicology? *Journal of Zoology*, **218**, 701–4.
- Calow, P. (ed.) (1993). *Handbook of ecotoxicology*, Vol. 1. Blackwell, Oxford.
- Calow, P. (ed.) (1994). *Handbook of ecotoxicology*, Vol. 2. Blackwell, Oxford.
- Cannon, R.J.C. (1983). Experimental studies on supercooling in two Antarctic micro-arthropods. *Journal of Insect Physiology*, **29**, 617–24.
- Cannon, R.J.C. (1986). Diet and acclimation effects on the cold tolerance and survival of an Antarctic springtail. *British Antarctic Survey Bulletin*, **71**, 19–30.
- Cannon, R.J.C. and Block, W. (1988). Cold tolerance of microarthropods. *Biological Reviews*, **63**, 23–77.
- Cannon, R.J.C., Block, W., and Collett, G.D. (1985). Loss of supercooling ability in *Cryptopygus antarcticus* (Collembola: Isotomidae) associated with water uptake. *Cryo-Letters*, **6**, 73–80.
- Carapelli, A., Fanciulli, P.P., Frati, F., and Dallai, R. (1995a). The use of genetic markers for the diagnosis of sibling species in the genus *Isotomurus* (Insecta, Collembola). *Bollettino di Zoologia*, **62**, 71–6.
- Carapelli, A., Frati, F., Fanciulli, P.P., and Dallai, R. (1995b). Genetic differentiation of six sympatric species of *Isotomurus* (Collembola, Isotomidae); is there any difference in their microhabitat preferences? *European Journal of Soil Biology*, **31**, 87–99.
- Carpenter, F.M. (1992). *Treatise on invertebrate paleontology*. Part R, Arthropoda 4, Volume 3: Superclass Hexapoda. Geological Society of America, University of Kansas, Boulder, Colorado (pp. 1–3 on Collembola).
- Carpenter, G.H. (1897). The Collembola of Mitchelstown cave. *Irish Naturalist*, **6**, 225–31, 257–8.
- Carpenter, G.H. (1921). Insecta Part 1. Collembola. British Museum (Natural History) British Antarctic ('Terra Nova') Expedition, 1910. Natural History Report. Zoology, Vol. III, No. 9, pp. 259–67.
- Carpenter, G.H. and Evans, W. (1899). The Collembola and Thysanura of the Edinburgh district. *Proceedings of the Royal Physical Society of Edinburgh*, **14**, 221–66.
- Carroll, S.B. (1995). Homeotic genes and the evolution of arthropods and chordates. *Nature*, **376**, 479–85.
- Carroll, S.B., Weatherbee, S.D., and Langeland, J.A. (1995). Homeotic genes and the regulation and evolution of insect wing number. *Nature*, **375**, 58–61.
- Cassagnau, P. (1953). Contribution à l'étude d'un collembole *Proctostephanus stuckeni*. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **88**, 39–58.
- Cassagnau, P. (1956). L'influence de la température sur l'apparition du 'genre' *Spinisotoma* (Collembola, Isotomidae). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **242**, 1531–4.
- Cassagnau, P. (1968a). L'évolution des pièces buccales et la polyténie chez les Collembola. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **267**, 106–9.
- Cassagnau, P. (1968b). *Neanurella microphthalma* n.g. n.sp. nouveau Collembola de l'île d'Eubée (Grèce). *Biologia Gallo-Hellenica*, **1**, 137–42.
- Cassagnau, P. (1968c). Les espèces européennes du genre *Bilobella* (Collembola, Neanuridae). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 2*, **40**, 292–307.
- Cassagnau, P. (1969). Sur un nouveau genre de Katiannini (Collembola Symphypleones) récolté en Grèce continentale. *Biologia Gallo-Hellenica*, **2**, 123–32.
- Cassagnau, P. (1971a). La phylogénie des Collembola à la lumière des structures endocrines retrocérébrales. I Symposium Internacional de Zoofilia. Facultad de Ciencias, Universidad de Salamanca, pp. 333–49.
- Cassagnau, P. (1971b). Les différents types d'ecomorphose chez les Collembola Isotomidae. *Revue d'Écologie et de Biologie du Sol*, **8**, 55–7.

- Cassagnau, P. (1971c). Le spermatophore des Collembolles Neanuridae. *Revue d'Écologie et de Biologie du Sol*, **8**, 609–16.
- Cassagnau, P. (1971d). Biologie de *Bilobella grassei* (Denis) dans la région toulousaine (Collembolles Neanuridae). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **107**, 279–94.
- Cassagnau, P. (1971e). Les chromosomes salivaires polytènes chez *Bilobella grassei* (Denis) (Collembolles: Neanuridae). *Chromosoma*, **35**, 57–83.
- Cassagnau, P. (1972a). Un Collembolle adapté à la prédation: *Cephalotoma grandiceps* (Reuter). *Nouvelle Revue d'Entomologie*, **2**, 5–12.
- Cassagnau, P. (1972b). Parthénogenèse géographique et polyploidie chez *Neanura muscorum* (Templeton), Collembolles Neanuridae. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **274**, 1846–8.
- Cassagnau, P. (1973). Sur un nouveau genre de Collembolles récolté en Grèce continentale et à Corfu. *Biologia Gallo-Hellenica*, **5**, 65–75.
- Cassagnau, P. (1974a). Adaptation écologique et morphogénèse: les écomorphoses. IX Congresso Nazionale Italiano di Entomologia, pp. 227–44. Bertelli and Piccardi, Florence.
- Cassagnau, P. (1974b). Les chromosomes polytènes de *Neanura monticola* Cassagnau (Collembolles). I. Polymorphisme écologique du chromosome X. *Chromosoma*, **46**, 343–63.
- Cassagnau, P. (1975). Le polymorphisme des chromosomes polytènes de *Bilobella aurantiaca* Caroli (Collembolles) et sa signification biogéographique et écologique. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **280D**, 2777–80.
- Cassagnau, P. (1976). La variabilité des chromosomes polytènes chez *Bilobella aurantiaca* Caroli (Collembolles Neanuridae) et ses rapports avec la biogéographie et l'écologie de l'espèce. *Archives de Zoologie Expérimentale et Générale*, **117**, 511–72.
- Cassagnau, P. (1977). Quelques problèmes relatifs aux critères spécifiques et à la spéciation chez les Collembolles. *Mémoires de la Société Zoologique de France*, **39**, 57–93.
- Cassagnau, P. (1978). Un nouveau genre de Collembolles Neanuridae du Sud de la Péninsule Ibérique: *Gamachorutes* n.g. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **114**, 17–26.
- Cassagnau, P. (1979). Les Collembolles Neanuridae des Pays Dinaro-Balkaniques: leur intérêt phylogénétique et biogéographique. *Biologia Gallo-Hellenica*, **8**, 185–203.
- Cassagnau, P. (1980a). Nouveaux critères pour un redécoupage phylogénétique des Collembolles Neanuridae (s. Massoud 1967). In *First International Seminar on Apterygota* (ed. R. Dallai), pp. 115–32. Accademia delle Scienze di Siena detta de' Fisiocritici, Siena.
- Cassagnau, P. (1980b). Sur le genre *Assamanura* n.g. du Nord-Est de l'Inde et sur la lignée Uchidanurienne (Collembolles). *Travaux du Laboratoire d'Écobiologie des Arthropodes Édaphiques, Toulouse*, **2**, (1), 1–7.
- Cassagnau, P. (1981). Les Collembolles du sol, marqueurs biogéographiques dans le subcontinent indien et l'Himalaya. *Cahiers Népalais, CNRS Greco 12*, 37–52.
- Cassagnau, P. (1982). Sur les Neanurinae primitifs suceurs et les lignées qui en dérivent (Collembolles). *Travaux du Laboratoire d'Écobiologie des Arthropodes Édaphiques, Toulouse*, **3**, (3), 1–11.
- Cassagnau, P. (1983a). Un nouveau modèle phylogénétique chez les Collembolles Neanurinae. *Nouvelle Revue d'Entomologie*, **13**, 3–27.
- Cassagnau, P. (1983b). Introduction à l'étude phylogénétique et biogéographique des Collembolles Neanurinae. *Pedobiologia*, **25**, 293–9.
- Cassagnau, P. (1984). Introduction à l'étude des Phylliomériens (Collembolles Neanurinae): diagnostics préliminaires des espèces. *Travaux du Laboratoire d'Écobiologie des Arthropodes Édaphiques, Toulouse*, **4**, (3), 1–30.
- Cassagnau, P. (1985). Le polymorphisme des femelles d'*Hydroisotoma schaefferi* (Krausb.): un nouveau cas d'épitoquie les Collembolles. *Annales de la Société Entomologique de France, N.S.*, **21**, 287–96.
- Cassagnau, P. (1986a). Sur l'évolution des Neanurinae paucitubercules à pièce buccales réduites (Collembolles). In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 313–17. University of Siena, Siena.
- Cassagnau, P. (1986b). Les écomorphoses des Collembolles. I. Déviation de la morphogénèse et perturbations histophysiologiques. *Annales de la Société Entomologique de France, N.S.*, **22**, 7–33.
- Cassagnau, P. (1986c). Les écomorphoses des Collembolles. II. Aspects phénologiques et analyse expérimentale des déterminismes. *Annales de la Société Entomologique de France, N.S.*, **22**, 313–18.
- Cassagnau, P. (1987). A propos des types de coloration chez *Isotomurus palustris* (Müller) (Collembolles). *Revue d'Écologie et de Biologie du Sol*, **24**, 85–9.
- Cassagnau, P. (1988). Les Collembolles Neanurinae des massifs du Sud de l'Inde et de Ceylan. *Travaux du Laboratoire d'Écobiologie des Arthropodes Édaphiques, Toulouse*, **5**, (4), 21–51.

- Cassagnau, P. (1989). Les Collembolles Neanurinae: elements pour une synthese phylogenetique et biogeographie. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 171–182. University of Siena, Siena.
- Cassagnau, P. (1990a). Des hexapodes vieux de 400 millions d'années: Les Collembolles. I. Biologie et evolution. II. Biogeographie et ecologie. *Année Biologique, Ser. 4*, **29**, 1–37, 39–69.
- Cassagnau, P. (1990b). Les Collembolles Neanurinae de l'Himalaya. I. Genres *Synameria*, *Singalimeria* et *Stenomeria*. *Annales de la Société Entomologique de France, N.S.*, **26**, 19–52.
- Cassagnau, P. (1991a). *Camerounura* n.g. n.sp. Collembol Neanurinae endémique du Mt. Cameroun. *Revue d'Écologie et de Biologie du Sol*, **28**, 221–4.
- Cassagnau, P. (1991b). Biogéographie des Collembolles Neanurinae des montagnes du Sud de l'Inde et de Sri Lanka. In *Advances in management and conservation of soil fauna* (ed. G.K. Veeresh, D. Rajagopal, and C.A. Viraktamath), pp. 39–45. Oxford and IBH, New Delhi.
- Cassagnau, P. (1991c). Les Collembolles Neanurinae de l'Himalaya. II. *Paranurini* et *Paleonurini* pancituberculés. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **6**, (4), 1–20.
- Cassagnau, P. (1993a). Les Collembolles Neanurinae de l'Himalaya. III. Genre *Nepalimeria*. *Revue Suisse de Zoologie*, **100**, 91–112.
- Cassagnau, P. (1993b). Les Collembolles de l'Himalaya. IV. Genres *Parvatina*, *Himaleria*, *Gnatholonche*. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **7**, (1), 1–38.
- Cassagnau, P. (1993c). Les Collembolles Neanurinae de l'Himalaya. V. Genres *Chaetobella*, *Travura*, *Adibolba*. *Annales de la Société Entomologique de France, N.S.*, **29**, 281–301.
- Cassagnau, P. and Dalens, H. (1976). Cycle phénologique et analyse expérimentale quelques caractères biologiques dans trois populations d'*Hypogastrura tullbergi* (Collembol). *Vie et Milieu*, **26**, 163–78.
- Cassagnau, P. and Deharveng, L. (1974). Les espèces Européennes du genre *Triacanthella* (Collembolles). *Nouvelle Revue d'Entomologie*, **4**, 165–80.
- Cassagnau, P. and Deharveng, L. (1976). Un nouveau sous-genre d'*Hypogastrura* (Collembolles) du Maroc: *Franzura synacantha* n.g. n.sp. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **112**, 199–203.
- Cassagnau, P. and Deharveng, L. (1980). Sur l'intérêt biogeographique et cytogénétique d'un nouveau genre de Collembol Neanuridae: le genre *Travura* n.g. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **2**, (2), 1–12.
- Cassagnau, P. and Deharveng, L. (1981). Sur le genre *Vitronura* (Collembolles Neanuridae): aspect systématique et approche cytogénétique. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, **3A**, 151–73.
- Cassagnau, P. and Deharveng, L. (1984). Collembolles des Philippines. I. Les Lobelliens multicolores des montagnes de Luzon. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **5**, (1), 1–11.
- Cassagnau, P. and Fabres, G. (1968). Contribution à l'étude des écomorphoses. III. Cycle phénologique et étude expérimentale chez deux espèces du genre *Isotoma* (Collembolles Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **3**, 455–91.
- Cassagnau, P. and Ferrero, M.J. (1966). Contribution à l'étude des écomorphoses. II. Phénologie comparée de quatre races d'*Hypogastrura purpurescens* (Collembolles, Poduromorphe). *Revue d'Écologie et de Biologie du Sol*, **3**, 223–40.
- Cassagnau, P. and Izarra, D.C. de (1969). Contribution à l'étude des écomorphoses. IV. Sur la signification de la forme *crassispina* chez *Ceratophysella armata* var. *attenuata* Cassagnau (Collembolles Poduromorphe). *Bulletin de la Société Zoologique de France*, **94**, 243–50.
- Cassagnau, P. and Juberthie, C. (1966). Neurosécrétion et organes endocrines chez *Tomocerus minor* (Collembolles). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **262**, 793–6.
- Cassagnau, P. and Juberthie, C. (1967a). Structures nerveuses, neurosécrétion et organes endocrines chez les Collembolles. I. Le complexe cérébral des Poduromorphes. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **103**, 178–222.
- Cassagnau, P. and Juberthie, C. (1967b). Structures nerveuses, neurosécrétion et organes endocrines chez les Collembolles. II. Le complexe cérébral des Entomobryomorphes. *General and Comparative Endocrinology*, **8**, 489–502.
- Cassagnau, P. and Lauga-Reyrel, F. (1984). L'architecture cuticulaire des Collembolles Neanurinae: présence d'un endosquelette superficiel chez certains d'entre-eux. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **299**, 591–6.
- Cassagnau, P. and Lauga-Reyrel, F. (1985). Sur la signification adaptative de l'architecture cuticulaire chez les Collembolles Arthropodées. *Revue d'Écologie et de Biologie du Sol*, **22**, 381–402.
- Cassagnau, P. and Lauga-Reyrel, F. (1987). Les caractéristiques de l'ecomorphose chez le Collembol *Isotomurus palustris* (Müller). *Revue d'Écologie et de Biologie du Sol*, **24**, 197–211.

- Cassagnau, P. and Lauga-Reyrel, F. (1992). Sur le polymorphisme et le cycle sexuel du Collembole *Superodontella lamellifera* (Axelson) dans les Pyrénées. *Annales de la Société Entomologique de France*, N.S., **28**, 371–84.
- Cassagnau, P. and Lee, B.H. (1982). Les chromosomes polytènes de *Paleonura spectabilis* Cass. (Collembolles Neanuridae). *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques*, Toulouse, **3**, (3), 12–18.
- Cassagnau, P. and Oliveira, E.P. de (1990). Les Collembolles Neanurinae d'Amerique du Sud. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **126**, 19–23.
- Cassagnau, P. and Oliveira, E.P. de (1992). Sur *Mastigoceras camponoti* Handschin, Collembole Orchesellinae d'Amazonie. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **128**, 27–31.
- Cassagnau, P. and Palacios-Vargas, J.G. (1983). Contribution à l'étude des Collembolles Neanurinae d'Amerique Latine. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques*, Toulouse, **4**, (1), 1–16.
- Cassagnau, P. and Raynal, G. (1964). Contribution à l'étude des écomorphoses. I. Développement comparé de deux races d'*Hypogastrura tullbergi* (Collembole Poduromorphe). *Revue d'Écologie et de Biologie du Sol*, **1**, 1–20.
- Cassagnau, P., Juberthie, C., and Raynal, G. (1968). Structures nerveuses, neurosécrétion et organes endocrines chez les Collembolles. III. Le complexe cérébral des Symphypleones. *General and Comparative Endocrinology*, **10**, 61–9.
- Cassagnau, P., Dallai, R., and Deharveng, L. (1979). Le polymorphisme des chromosomes polytènes de *Lathriopyga longiseta* Caroli (Collembole Neanuridae). *Caryologia*, **32**, 461–83.
- Cassagnau, P., Deharveng, L., and Peja, N. (1985). La différenciation des caryotypes polytènes dans le genre *Bilobella* (Collembolles Neanurinae). *Génétique, Sélection, Evolution*, **17**, 1–24.
- Chakravorty, P.P. and Joy, V.C. (1990). Ill effects of Monocil (Monocrotophos) on the nontarget soil microarthropods. *Journal of Environmental Biology*, **11**, 127–36.
- Chapman, P.M., Caldwell, R.S., and Chapman, P.F. (1996). A warning: NOECs are inappropriate for regulatory use. *Environmental Toxicology and Chemistry*, **15**, 77–9.
- Chaudonneret, J. (1987). Evolution of the insect brain with special reference to the so-called tritocerebrum. In *Arthropod brain* (ed. A.P. Gupta), pp. 3–26. John Wiley, New York.
- Chauvin, G. and Vannier, G. (1989). Resistance au froid et repletion du tube digestif chez *Allacma fusca* (Collembola, Symphypleona) et *Tinea pellionella* (Lepidoptera, Tineidae). *Bulletin de la Société Zoologique de France*, **114**, 111–18.
- Chelnokov, V.G. (1987). New species of springtails of the genus *Entomobrya* Rondani (Collembola, Entomobryidae) from the north east of the USSR. *Entomologicheskoe Obozrenie*, **66**, 96–101.
- Chelnokov, V.G. (1990). A new genus, new and little known species of springtails (Collembola) in the fauna of northeast Asia. *Entomologicheskoe Obozrenie*, **69**, 342–52.
- Chen, B., Snider, R.J., and Snider, R.M. (1995). Food preference and effects of food type on the life history of some soil Collembola. *Pedobiologia*, **39**, 496–505.
- Chen, B., Snider, R.J., and Snider, R.M. (1996). Food consumption by Collembola from northern Michigan deciduous forest. *Pedobiologia*, **40**, 149–61.
- Chen, J.X. and Christiansen, K. (1993). The genus *Sinella* with special reference to *Sinella* s.s. (Collembola: Entomobryidae) of China. *Oriental Insects*, **27**, 1–54.
- Cheng, L. and Frank, J.H. (1993). Marine insects and their reproduction. *Oceanography and Marine Biology Annual Reviews*, **31**, 479–506.
- Chiba, S. (1976). Studies on the productivity of soil animals in Pasoh Forest Reserve, West Malaysia. III. a turnover of the generation of a tropical springtail (Collembola: Entomobryidae). *Scientific Reports of Hirosaki University*, **23**, 79–83.
- Chiba, Y., Cutkomp, L.K., and Halberg, F. (1973). Circaseptan (7 day) oviposition rhythm and growth of springtail *Folsomia candida* (Collembola: Isotomidae). *Journal of Interdisciplinary Cycle Research*, **4**, 59–66.
- Choudhuri, D.K. (1961). Influence of temperature on the sex ratio of *Onychiurus imperfectus* Denis (Collembola). *Science and Culture*, **27**, 48–9.
- Choudhuri, D.K. (1962). Collembolan aggregations in a single forest habitat and their variance. *Science and Culture*, **28**, 490–1.
- Choudhuri, D.K. (1963). Revision of Bagnall's work on the genus *Onychiurus* (Collembola). *Proceedings of the National Academy of Sciences, India*, **33B**, 329–41.
- Christian, E. (1978). The jump of springtails. *Naturwissenschaften*, **65**, 495–6.
- Christian, E. (1979). Der Sprung des Collembolen. *Zoologische Jahrbücher für Physiologie*, **83**, 457–90.
- Christian, E. (1983). Variation in eye numbers in Austrian cave populations of *Bonetogastrura cavicola* (Collembola, Hypogastruridae). *Pedobiologia*, **25**, 266.

- Christian, E. (1985a). Zur Collembolenfauna eines Permafrostbodens in der Karawanken-Nordkette. *Carinthia II, Klagenfurt*, **175/95**, 141–49.
- Christian, E. (1985b). Springschwänze (Collembolen) aus Vorarlberg. *Jahrbuch des Vorarlberger Landesmuseumsvereins*, **1984**, 83–89.
- Christian, E. (1986a). Verbreitung und Taxonomie der europäischen *Appendisotoma*-Arten (Hex., Collembola, Isotomidae). *Mitteilungen der Abteilung für Zoologie am Landesmuseum Joanneum*, **39**, 5–9.
- Christian, E. (1986b). Apterygota from terrestrial sand, gravel, and debris accumulations in Austria. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 139–41. University of Siena, Siena.
- Christian, E. (1986c). *Micranurophorus schalleri* n.sp. aus dem terrestrischen Sandlückensystem des Neusiedlersee-Ufers (Collembola, Isotomidae). *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich*, **124**, 121–8.
- Christian, E. (1986d). *Onychiurus (Oligaphorura) hackeri* n.sp., ein cavernicoler Springschwanz aus Niederösterreich (Hexapoda: Collembola). *Annalen des Naturhistorischen Museums, Wien*, **87B**, 177–80.
- Christian, E. (1987). Collembola (Springschwänze). *Catalogus Faunae Austriae*, **12A**, 1–80.
- Christian, E. (1988). Induction and detection of moulting synchronization in *Folsomia candida* laboratory populations (Collembola: Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **25**, 469–78.
- Christian, E. (1989a). Biogeography, substrate preference, and feeding types of North Adriatic intertidal Collembola. *P.S.Z.N.I. Marine Ecology*, **10**, 79–94.
- Christian, E. (1989b). Position, structure and systematic significance of anal valve pseudocelli in onychiurid Collembola. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 43–6. University of Siena, Siena.
- Christian, E. (1990). Ein nicht-myzelialer Pilz (*Amphoromorpha*) als Ektoparasit an Höhlen-Collembolen. *Carinthia II, Klagenfurt*, **180/100**, 373–80.
- Christian, E. (1993a). Collembolen aus zwei Windröhren des Ötscherlandes (Niederösterreich). *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich*, **130**, 157–69.
- Christian, E. (1993b). Pilze als Endokommensalen im Darm von Collembolen (Trichomycetes, *Orchesellaria*). *Linzer Biologische Beiträge*, **25**, 51–6.
- Christian, E. (1994). Vom Leben unter der Erde: Die Kleintierwelt niederösterreichischer Höhlen. In *Faszination Höhle-Höhlen und Höhlenforschung in Niederösterreich* (ed. E. Steiner), pp. 43–9. Katalog der Niederösterreich Landesmuseum N.F. 361, Wien.
- Christian, E. and Kamplichr, C. (1984). Zur Zoogeographie einiger epedaphischer Collembolen aus dem östlichen Niederösterreich. *Annalen des Naturhistorischen Museums, Wien*, **86B**, 133–9.
- Christian, E. and Schaller, F. (1982). Die Augen-Variabilität bei *Bonetogastrura cavicola* (Börner 1901): Eidonomische, topographische und numerische Variabilität (Collembola: Hypogastruridae). *Zoologischer Anzeiger*, **209**, 47–59.
- Christian, E. and Thibaud, J.M. (1988). Terrestrisch-interstitielle Collembolen aus österreichischen und ungarischen Sanden. *Pedobiologia*, **31**, 229–37.
- Christian, E. and Völlenkle, W. (1979). Collembolensprung-Absprung bei *Heteromurus*, *Lepidocyrtus*, *Isotoma* und *Hypogastrura*. *Wissenschaftliche Film (Wien)*, **23**, 11–18.
- Christiansen, K. (1958a). The Entomobryiform male genital plate. *Proceedings of the Iowa Academy of Science*, **65**, 474–6.
- Christiansen, K. (1958b). Geographic variation and the subspecies concept in the collembolan *Entomobryoides guthrei*. *Systematic Zoology*, **7**, 10–15.
- Christiansen, K. (1961). Convergence and parallelism in cave Entomobryinae. *Evolution*, **15**, 288–301.
- Christiansen, K. (1964a). Bionomics of Collembola. *Annual Review of Entomology*, **9**, 147–78.
- Christiansen, K. (1964b). A revision of the Nearctic members of the genus *Tomocerus* (Collembola, Entomobryidae). *Revue d'Écologie et de Biologie du Sol*, **1**, 639–78.
- Christiansen, K. (1965). Behaviour and form in the evolution of cave Collembola. *Evolution*, **19**, 529–37.
- Christiansen, K. (1966). The genus *Arrhopalites* (Collembola: Sminthuridae) in the United States and Canada. *International Journal of Speleology*, **2**, 43–73.
- Christiansen, K. (1967). Competition between collembolan species in culture jars. *Revue d'Écologie et de Biologie du Sol*, **4**, 439–62.
- Christiansen, K.A. (1970a). Invertebrate populations in the Moulis Cave. *Annales de Spéléologie*, **25**, 244–73.
- Christiansen, K. (1970b). Survival of Collembola on clay substrates with and without food added. *Annales de Spéléologie*, **25**, 849–52.
- Christiansen, K. (1970c). Experimental studies on the aggregation and dispersal of Collembola. *Pedobiologia*, **10**, 180–98.
- Christiansen, K. (1971a). Factors affecting predation on Collembola by various arthropods. *Annales de Spéléologie*, **26**, 97–106.

- Christiansen, K. (1971b). Notes on Miocene amber Collembola from Chiapas. *University of California Publications in Entomology*, **65**, 645–8.
- Christiansen, K.A. (1980). A new nearctic species of the genus *Tomocerus* (Collembola: Entomobryidae). *Proceedings of the Iowa Academy of Science*, **87**, 121–3.
- Christiansen, K. (1982a). Zoogeography of cave Collembola east of the Great Plains. *Natural Science Series Bulletin*, **44**, 32–41.
- Christiansen, K. (1982b). Notes on Mexican cave *Pseudosinella* (Collembola: Entomobryidae) with the description of six new species. *Folia Entomológica Mexicana*, **53**, 3–5.
- Christiansen, K. (1985). Regressive evolution in Collembola. *Natural Science Series Bulletin*, **47**, 89–100.
- Christiansen, K. (1990). Insecta: Collembola. In *Soil biology guide* (ed. D.L. Dindal), pp. 965–95. John Wiley, New York.
- Christiansen, K. (1992a). Springtails. *Kansas School Naturalist*, **39**, 3–16.
- Christiansen, K. (1992b). Biological processes in space and time: cave life in the light of modern evolutionary theory. In *The natural history of biospeleology* (ed. A. Camacho), pp. 453–72. Monografías del Museo Nacional de Ciencias Naturales, Madrid.
- Christiansen, K. and Bellinger, P. (1980). *The Collembola of North America, north of the Rio Grande*. Grinnell College, Grinnell, Iowa.
- Christiansen, K. and Bellinger, P. (1988). Marine littoral Collembola of North and Central America. *Bulletin of Marine Science*, **42**, 215–45.
- Christiansen, K.A. and Bellinger, P.F. (1991). Phylogeny of the Hawaiian species of the genus *Lepidocyrtus* (Collembola, Entomobryidae). *Revue d'Écologie et de Biologie du Sol*, **28**, 207–15.
- Christiansen, K. and Bellinger, P. (1992). *Insects of Hawaii, Volume 15, Collembola*. University of Hawaii Press, Honolulu.
- Christiansen, K. and Bellinger, P. (1994). Biogeography of Hawaiian Collembola: the simple principles and complex reality. *Oriental Insects*, **28**, 309–51.
- Christiansen, K. and Bouillion, M. (1978a). An evolutionary and ecological analysis of the terrestrial arthropods of caves in the Central Pyrenees. Part One: Ecological analysis with special reference to Collembola. *National Speleological Society Bulletin*, **40**, 103–13.
- Christiansen, K. and Bouillion, M. (1978b). An evolutionary and ecological analysis of the terrestrial arthropods of caves in the Central Pyrenees. Part Two: Evolutionary analysis of three species of Collembola. *National Speleological Society Bulletin*, **40**, 114–17.
- Christiansen, K. and Culver, D. (1968). Geographic variation and evolution in *Pseudosinella hirsuta*. *Evolution*, **22**, 237–55.
- Christiansen, K. and Culver, D. (1969). Geographic variation and evolution in *Pseudosinella violenta*. *Evolution*, **23**, 602–21.
- Christiansen, K. and Culver, D. (1987). Biogeography and the distribution of cave Collembola. *Journal of Biogeography*, **14**, 459–77.
- Christiansen, K.A. and Luther, G. (1986). Two new species of Hawaiian *Pseudosinella* (Collembola: Entomobryomorpha: Entomobryidae). *Proceedings of the Hawaiian Entomological Society*, **26**, 45–51.
- Christiansen, K. and Moberg, T. (1988). *Pseudosinella* revisited (Collembola, Entomobryinae). *International Journal of Speleology*, **17**, 1–20.
- Christiansen, K. and Reddell, J.R. (1986). The cave Collembola of Mexico. *Texas Memorial Museum, Speleological Monograph*, **1**, 127–162.
- Christiansen, K., Lyman, S., and Johnson, D. (1972). Contact behaviour in Collembola and the effect of food deprivation, density and culture origins. *Pedobiologia*, **12**, 222–8.
- Christiansen, K., Gama, M.M. da, and Bellinger, P. (1983). A catalogue of the species of the genus *Pseudosinella*. *Ciência Biológica (Portugal)*, **5**, 13–31.
- Christiansen, K.A., Bellinger, P.F., and Gama, M.M. da (1990). Computer assisted identification of specimens of *Pseudosinella* (Collembola, Entomobryidae). *Revue d'Écologie et de Biologie du Sol*, **27**, 231–46.
- Christiansen, K., Doyle, M., Kahlert, M., and Gobaleza, D. (1992). Interspecific interactions between collembolan populations in culture. *Pedobiologia*, **36**, 274–86.
- Coates, T.J. (1968a). The Collembola of South Africa. 1. The genus *Neanura*. *Journal of the Entomological Society of Southern Africa*, **31**, 185–95.
- Coates, T.J. (1968b). The Collembola of South Africa. 2. The genus *Seira*. *Journal of the Entomological Society of Southern Africa*, **31**, 435–62.
- Coates, T.J. (1969). The Collembola of South Africa. 3. The genus *Lepidokrugeria*. *Journal of the Entomological Society of Southern Africa*, **32**, 87–9.
- Cole, F.J. (1949). *A history of comparative anatomy from Aristotle to the eighteenth century*. Macmillan, London.

- Coleman, D.C. and Macfadyen, A. (1966). The recolonisation of gamma-irradiated soil by small arthropods. *Oikos*, **17**, 62–70.
- Colinas, C., Ingham, E., and Molina, R. (1994). Population responses of target and non-target forest soil organisms to selected biocides. *Soil Biology and Biochemistry*, **26**, 41–7.
- Convey, P. (1992). Seasonal lipid contents of Antarctic microarthropods. *Experimental and Applied Acarology*, **15**, 219–31.
- Convey, P. (1994). The use of field enclosures to measure growth and mortality rates in an Antarctic collembolan. *Acta Zoologica Fennica*, **195**, 18–22.
- Coope, G.R. (1995). The effects of quaternary climate changes on insect populations: lessons from the past. *Symposia of the Royal Entomological Society of London*, **17**, 29–48.
- Cox, P. (1982). The Collembola fauna of North and Northwestern Iran. *Entomologist's Monthly Magazine*, **118**, 39–43.
- Cracraft, J. (1994). Species diversity, biogeography and the evolution of biotas. *American Zoologist*, **34**, 33–47.
- Cragg, J.B. (1961). Some aspects of the ecology of moorland animals. *Journal of Animal Ecology*, **30**, 205–34.
- Cranston, P.S., Gullan, P.J., and Taylor, R.W. (1991). Principles and practice of systematics. In *The Insects of Australia* Volume 1 (2nd edn) (ed. CSIRO), pp. 109–24. Carlton: Melbourne University Press.
- Cromack, K., Sollins, P., Todd, R.L., Crossley, D.A., Fender, W.M., Fogel, R., and Todd, A.W. (1977). Soil microorganism-arthropod interactions: fungi as major calcium and sodium sources. In *The role of arthropods in forest ecosystems* (ed. W.J. Mattson), pp. 78–84. Springer Verlag, New York.
- Crommentuijn, T. (1994). *Sensitivity of soil arthropods to toxicants*. PhD thesis, Free University, Amsterdam.
- Crommentuijn, T., Brils, J., and Van Straalen, N.M. (1993). Influence of cadmium on life-history characteristics of *Folsomia candida* (Willem) in an artificial soil substrate. *Ecotoxicology and Environmental Safety*, **26**, 216–27.
- Crommentuijn, T., Doodeman, C.J.A.M., Doornekamp, A., Van der Pol, J.J.C., Bedaux, J.J.M., and Van Gestel, C.A.M. (1994). Lethal body concentrations and accumulation patterns determine time-dependent toxicity of cadmium in soil arthropods. *Environmental Toxicology and Chemistry*, **13**, 1781–9.
- Crommentuijn, T., Stab, J.A., Doornekamp, A., Estoppey, O., and Van Gestel, C.A.M. (1995). Comparative ecotoxicity of cadmium, chlorpyrifos and triphenyltin hydroxide for four clones of the parthenogenetic collembolan *Folsomia candida* in an artificial soil. *Functional Ecology*, **9**, 734–42.
- Crouau, Y., Bauby, A., and Deharveng, L. (1987). Fine structure of the tibiotarsal and pretarsal sensory organs in *Monobella grassei banyulensis* Deharveng (Collembola, Neanuridae). *International Journal of Insect Morphology and Embryology*, **16**, 245–61.
- Culik, M. and Deharveng, L. (1986). First record of the marine intertidal collembolan *Xenylla affinisformis* (Hypogastruridae) for North America. *Entomological News*, **97**, 201–2.
- Culik, M. and Najt, J. (1986). Ecomorphosis in *Folsomia elongata* MacGillivray, 1896 (Collembola, Isotomidae). *Journal of the Kansas Entomological Society*, **59**, 395–7.
- Curl, E.A. (1988). The role of microfauna in plant-disease suppression. *CRC Critical Reviews in Plant Sciences*, **7**, 175–96.
- Curl, E.A. and Snell, J.M. (1981). Grazing patterns of mycophagous Collembola and assessment of biocontrol potential. *Phytopathology*, **71**, 869.
- Curl, E.A., Harper, J.D., Peterson, C.M., and Gudauskas, R.T. (1985). Relationships of mycophagous Collembola and *Rhizoctonia solani* populations in biocontrol. *Phytopathology*, **75**, 1360.
- Curl, E.A., Lartey, R., and Peterson, C.M. (1988). Interactions between root pathogens and soil microarthropods. *Agriculture, Ecosystems and Environment*, **24**, 249–61.
- Curry, J.P. (1969). The qualitative and quantitative composition of the fauna of an old grassland site at Celbridge, Co. Kildare. *Soil Biology and Biochemistry*, **1**, 219–27.
- Curry, J.P. (1971). Seasonal and vertical distribution of the arthropod fauna of an old grassland soil. *Scientific Proceedings of the Royal Dublin Society*, **3B**, (4), 49–71.
- Curtis, J. (1860). *Farm insects*. Blackie, Oxford.
- Cutkomp, L.K., Marques, M.D., Halberg, F., Cornelissen, G., and Marques, N. (1987a). Springtails: a model for the study of spectral structure and beneficial circadian-circaseptan synchronizer manipulation. *Chronobiologia*, **14**, 166–7.
- Cutkomp, L.K., Marques, M.D., Snider, R., Cornelissen, G., Wu, J., and Halberg, F. (1987b). Chronobiologic view of moult and longevity of *Folsomia candida* (Collembola) at different ambient temperatures. In *Advances in chronobiology*, Part A, pp. 249–256. A.R. Liss, New York.
- Cuvier, G. and Latreille, P.A. (1838–1849). *La règne animal, distribué d'après son organisation*. Déterville, Paris.

- Czarnecki, A. and Losinski, J. (1985). The effect of GT seed dressing on the community of Collembola in the soil under sugar beet. *Pedobiologia*, **28**, 427–31.
- Dalens, H. (1982). Free amino acids in two populations of the Collembola *Hypogastrura tullbergi* (Schaffer). *Revue d'Écologie et de Biologie du Sol*, **19**, 251–8.
- Dalens, H. and Najt, J. (1981). Biochemical fingerprints as indicators of the ecomorphic phenotype of the collembolan *Isotoma tigrina*. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, Ser. 3, **293**, 471–3.
- Dalens, H. and Rousset, A. (1986). Polymorphisme physiologique de l'activité esterase au cours du cycle de mue chez *Hypogastrura boldrii*. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 181–6. University of Siena, Siena.
- Dalens, H. and Rousset, A. (1988). Variations in esterase activity among *Hypogastrura* species of the sub-group *tullbergi* (Collembola). *Revue d'Écologie et de Biologie du Sol*, **25**, 139–47.
- Dalens, H. and Vannier, G. (1979). Ecomorphose et rétention hydrique chez le collembole *Hypogastrura tullbergi* (Schäffer). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **289D**, 931–3.
- Dalla Torre, K.W. (1895). Die Gattungen und Arten der Apterygogenea (Brauer). *Programm k.k. Staats-Gymnasium Innsbruck*, **46**, 1–23.
- Dallai, R. (1967a). Intranuclear vesiculation in Collembola. *Monitore Zoologico Italiano*, (N.S.), **1**, 101–8.
- Dallai, R. (1967b). Lo spermatozoo degli Arthropodi. I. *Anurida maritima* (Guérin) ed *Orchesella cincta* (Geoffroy) (Insecta, Collembola). *Atti dell'Accademia dei Fisiocritici*, Ser. 13, **16**, 468–76.
- Dallai, R. (1968). Ricerche sui Collemboli. III. Nuovi reperti sull'Isola d'Ischia. *Atti dell'Accademia dei Fisiocritici*, Ser. 13, **17**, 92–105.
- Dallai, R. (1969a). Ricerche sui Collemboli. V. L'Isola di Montecristo. *Redia*, **51**, 229–50.
- Dallai, R. (1969b). Ricerche sui Collemboli. VI. Le Isole di Capraia e di Pianosa. *Redia*, **51**, 277–304.
- Dallai, R. (1970a). Ricerche sui Collemboli. IX. Contributo alla conoscenza di *Disparrrhopalites patrizii* (Cassagnau e Delamare, 1953). *Redia*, **52**, 149–60.
- Dallai, R. (1970b). Investigations on Collembola. 10. Examination of the cuticle of some species of the tribe Sminthurini Börner, 1913, by means of the scanning electron microscope. *Monitore Zoologico Italiano*, (N.S.), **4**, 41–53.
- Dallai, R. (1970c). The spermatozoon of Arthropoda. XI. Further observations on Collembola. In *Comparative spermatology* (ed. B. Baccetti), pp. 275–9. Academic Press, London.
- Dallai, R. (1971a). First data on the ultrastructure of the postantennal organ of Collembola. *Revue d'Écologie et de Biologie du Sol*, **8**, 11–29.
- Dallai, R. (1971b). Ricerche sui Collemboli. XV. Monti reatini ed Alcuni Rilievi Abruzzesi. *Lavori della Società Italiana di Biogeografia*, (N.S.), **2**, 323–77.
- Dallai, R. (1972). La cuticola degli Sminthurini al microscopio elettronico a scansione. *Atti del IX Congresso Nazionale Italiano di Entomologia*, pp. 217–26. Bertelli and Piccardi, Firenze.
- Dallai, R. (1973a). Ricerche sui Collemboli. XVI. *Stachorutes dematteisi* n.gen, n.sp., *Micranurida intermedia* n.sp. e considerazioni sul genere *Micranurida*. *Redia*, **54**, 23–31.
- Dallai, R. (1973b). Ricerche sui Collemboli. XVIII. La cuticola e gli gnatidi di *Tetradontophora bielensis* (Waga) al microscopio elettronico a scansione. *Redia*, **54**, 105–16.
- Dallai, R. (1974a). Spermatozoa and phylogenesis. A few data on Insecta Apterygota. *Pedobiologia*, **14**, 148–56.
- Dallai, R. (1974b). New observations on Sminthurini cuticle. *Pedobiologia*, **14**, 313–22.
- Dallai, R. (1975a). Continuous and gap junction in the midgut of Collembola as revealed by lanthanum tracer and freeze-etching techniques. *Journal of Submicroscopic Cytology*, **7**, 249–57.
- Dallai, R. (1975b). Ultrastructural and polarized light microscope studies on spermatophores of *Dicyrtoma ornata* (Insecta, Collembola). *Journal of Ultrastructural Research*, **50**, 355–61.
- Dallai, R. (1977). Considerations on the cuticle of Collembola. *Revue d'Écologie et de Biologie du Sol*, **14**, 117–24.
- Dallai, R. (1978). Ricerche sui Collemboli. XXIII. Una nuova specie cavernicola della Sicilia. *Animalia (Catania)*, **5**, 345–55.
- Dallai, R. (1979a). An overview of atypical spermatozoa in insects. In *The Spermatozoon* (ed. D.W. Fawcett and J.M. Bedford), pp. 253–65. Urban and Schwarzenberg Inc., Baltimore-Munich.
- Dallai, R. (1979b). Investigations on Collembola. XXIV. On the systematics of Neelidae with redescription of *Neelides folsomi* Caroli. *Animalia (Catania)*, **6**, 271–81.
- Dallai, R. (1979c). Polytene chromosomes of some *Bilobella aurantiaca* (Collembola) Italian populations. *Bollettino di Zoologia*, **46**, 231–49.
- Dallai, R. (1980a). Considerations on Apterygota phylogeny. *Bollettino di Zoologia*, **47**, 35–48.

- Dallai, R. (1980b). Collemboli e Proturi alla ribalta delle ricerche entomologiche. *Atti dell'Accademia Nazionale Italiana di Entomologia*, **28/29**, 3–31.
- Dallai, R. (1980c). The pyloric region of Collembola and Protura. In *First International Seminar on Apterygota* (ed. R. Dallai), pp. 175–7. Accademia delle Scienze di Siena detta de'Fisiocritici, Siena.
- Dallai, R. (1981). Recherches sur les Collemboles. 27. Une espèce nouvelle de Bovicornia de la Somalie. *Monitore Zoologico Italiano*, (N.S.), Supplemento, **14**, 241–59.
- Dallai, R. (1983). Interesse biogeografico dei Neanuridi (Collembola) della Sardegna e delle isole dell'Arcipelago Toscano. *Lavori della Società Italiana di Biogeografia*, (N.S.), **8**, 417–65.
- Dallai, R. (ed.) (1986). *Second International Seminar on Apterygota*. University of Siena, Siena.
- Dallai, R. (ed.) (1989). *Third International Seminar on Apterygota*. University of Siena, Siena.
- Dallai, R. (1994a). Recent findings on apterygoten sperm structure. *Acta Zoologica Fennica*, **195**, 23–7.
- Dallai, R. (1994b). An unusual terminal web structure in the midgut cells of the collembolan *Isotomurus*. In *The development of science for the improvement of human life* (Second Kyoto-Siena Symposium), pp. 112–121. Kyoto.
- Dallai, R. and Callaini, G. (1979). Comparative analysis of the Collembolan pyloric region (Insecta Apterygota). *Monitore Zoologico Italiano*, (N.S.), **13**, 45–66.
- Dallai, R. and Fanciulli, P.P. (1982). I cromosomi politenici di alcune popolazioni di *Lathriopyga longiseta* (Insecta, Collembola) della Toscana meridionale. *Redia*, **65**, 9–28.
- Dallai, R. and Fanciulli, P.P. (1983). Ricerche sui Collemboli. XXX. Un nuovo genere di Neanuride del Cansiglio (Prealpi Venete). *Redia*, **66**, 235–44.
- Dallai, R. and Fanciulli, P.P. (1985). A new species of *Temeritas* (Insecta, Collembola) from China. *Entomotaxonomia*, **7**, 157–64.
- Dallai, R. and Ferrari, R. (1970). Ricerche sui Collemboli. XI. Nuove osservazioni morfologiche e corologiche su *Hypogastrura* (s.str) *socialis* (Uzel) e *Hypogastrura* (s.srt.) *meridionalis*. *Redia*, **52**, 161–75.
- Dallai, R. and Malatesta, E. (1973). Ricerche sui Collemboli. XIX. La fine struttura epicuticolare di *Podura* ed *Actaetes*. *Redia*, **54**, 135–9.
- Dallai, R. and Malatesta, E. (1982). Collemboli cavernicoli Italiani (Ricerche sui Collemboli XXVI). *Lavori della Società Italiana di Biogeografia*, (N.S.), **7**, 173–94.
- Dallai, R. and Martinozzi, I. (1980). Ricerche sui Collemboli. XXV. La Val di Farma. *Atti dell'Accademia dei Fisiocritici*, Ser. 14, **12**, 1–51.
- Dallai, R. and Mohamed, A.M. (1981). Ricerche sui Collemboli. XXIX. Prima segnalazione del maschio di *Collophora*. *Redia*, **64**, 263–7.
- Dallai, R. and Sabatini, M.A. (1981). Ricerche sui Collemboli. XXVIII. Si di una nuova specie endogea di *Schaefferia*. *Redia*, **64**, 195–204.
- Dallai, R., Sbordoni, V., Cobolli Sbordoni, M., and De Matthaes, E. (1983). Chromosome and enzyme diversity in some species of Neanuridae (Collembola). *Pedobiologia*, **25**, 301–11.
- Dallai, R., Fanciulli, P.P., and Petrucci, R. (1986). Enzyme diversity in the genus *Bilobella* (Insecta, Collembola). *Revue d'Écologie et de Biologie du Sol*, **23**, 333–48.
- Dallai, R., Malatesta, E., and Focardi, S. (1988). On two Antarctic Collembola, *Gressittacantha terranova* and *Friesia grisea*. *Revue d'Écologie et de Biologie du Sol*, **25**, 365–72.
- Dallai, R., Callaini, G., and Lupetti, P. (1989). New observations on Collembola midgut. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 207–14. University of Siena, Siena.
- Dallai, R., Trastullo, E., Lupetti, P., and Mencarelli, C. (1993). Unusual cytoskeletal association with the intercellular septate junction in the midgut of Collembola (Insecta: Apterygota). *International Journal of Insect Morphology and Embryology*, **22**, 473–86.
- Dallai, R., Malatesta, E., and Ramellini, P. (1995). Apterygota: Collembola, Protura, Microcoryphia e Zygentoma (= Thysanura s.l.), Diplura. *Checklist delle specie della fauna italiana* (ed. A. Minelli, S. Ruffo, and S. La Posta), **33**. Calderini, Bologna.
- Dallinger, R. (1993). Strategies of metal detoxification in terrestrial invertebrates. In *Ecotoxicology of metals in invertebrates* (ed. R. Dallinger and P.S. Rainbow), pp. 245–89. Lewis, Chelsea, USA.
- Danks, H.V. (1981). *Arctic arthropods. A review of systematics and ecology with particular reference to the North American fauna*. Entomological Society of Canada, Ottawa.
- Danks, H.V. (1992). Arctic insects as indicators of environmental change. *Arctic*, **45**, 159–66.
- Darwin, C.R. (1871). *The descent of Man*. John Murray, London.
- Dasgupta, R. and Dasgupta, B. (1990). Collembolan insects as potential parasites. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **84**, 438.
- Davidson, J. (1933a). The environmental factors affecting the development of the eggs of *Sminthurus viridis* L. (Collembola). *Australian Journal of Experimental Biology and Medical Science*, **11**, 9–23.

- Davidson, J. (1933b). The distribution of *Sminthurus viridis* L. (Collembola) in South Australia, based on rainfall, evaporation and temperature. *Australian Journal of Experimental Biology and Medical Science*, **11**, 59–66.
- Davidson, J. (1934). The 'Lucerne Flea' *Sminthurus viridis* L. (Collembola) in Australia. *Council for Scientific and Industrial Research, Melbourne*, **79**, 1–66.
- Davies, M. (1967). A woodland floor food chain in the laboratory. *Entomologist's Monthly Magazine*, **103**, 187–9.
- Davies, W.M. (1925). Investigations of springtails attacking mangolds. *Journal of the Ministry of Agriculture*, **32**, 350–4.
- Davies, W.M. (1926). Collembola injuring leaves of mangold seedlings. *Bulletin of Entomological Research*, **17**, 159–62.
- Davies, W.M. (1927). On the tracheal system of Collembola with special reference to that of *Sminthurus viridis*. *Quarterly Journal of Microscopical Science*, **71**, 15–30.
- Davies, W.M. (1928a). On the economic status and bionomics of *Sminthurus viridis*. *Bulletin of Entomological Research*, **18**, 291–6.
- Davies, W.M. (1928b). The effect of variation in relative humidity on certain species of Collembola. *British Journal of Experimental Biology*, **6**, 79–86.
- Davis, B.N.K. (1963). A study of micro-arthropod communities in mineral soils near Corby, Northants. *Journal of Animal Ecology*, **32**, 49–71.
- Davis, D.H.S. (1934). A preliminary study of the nest fauna of the short-tailed voles (*Microtus agrestis* and *M. hirsutus*). *Entomologist's Monthly Magazine*, **70**, 96–101.
- Debruyne, L. (1988). Habitat selection and circadian rhythm of the intertidal collembolan *Anurida maritima* (Guerin) (Collembola, Poduridae). *Annales de la Société Royale Zoologique de Belgique*, **118**, 78.
- De Geer, C. (1743). Beskrifning pæn Insect, kallad: *Podura fusca*, *globosa*, *nitida*, *antennis longis articulus plurimis*. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **4**, 296–305.
- De Geer, C. (1744). Experimenta et observationes de parvulis insectis, agili saltu corpuscular sua in altum levantibus, quibus Podurae nomen est, exhibitae. *Acta Societatis Regiae Scientiarum Upsaliensis*, **1740**, 48–67.
- De Geer, C. (1778). *Memoires pour servir à l'histoire des insectes*. Volume 7. Pierre Hesselberg, Stockholm.
- Deharveng, L. (1976a). Presence d'un caractère sexuel secondaire chez *Anurophorus serratus* n.sp. (Collembola: Isotomidae). *Nouvelle Revue d'Entomologie*, **6**, 109–11.
- Deharveng, L. (1976b). L'écologie de *Neanura* (*Lathriopyga*) *monticola* (Collembola) dans les forêts du Val d'Aran et sa traduction cytogénétique. *Vie et Milieu*, **26**, 77–90.
- Deharveng, L. (1977). Étude chaetotaxique des Collembolles Isotomidae. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 3, Zoologie*, **318**, 597–619.
- Deharveng, L. (1978). Contribution à l'étude des Anurophorinae à épines anales (Collembola, Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **15**, 551–73.
- Deharveng, L. (1979a). Collembolles cavernicoles. III. *Onychiurus ariegicus* n.sp. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **115**, 378–82.
- Deharveng, L. (1979b). Chétotaxie sensillaire et phylogenèse chez les Collembolles Arthropleona. *Travaux du Laboratoire d'Écobiologie des Arthropodes Édaphiques, Toulouse*, **1**, (3), 1–15.
- Deharveng, L. (1979c). Contribution à la connaissance des Collembolles Neanurinae de France et de la Péninsule Ibérique. *Travaux du Laboratoire d'Écobiologie des Arthropodes Édaphiques, Toulouse*, **1**, (4), 1–61.
- Deharveng, L. (1980a). Note sur un type d'organites tegumentaires originaux recontre chez les Isotomidae (Collembola). In *First International Seminar on Apterygota* (ed. R. Dallai), pp. 59–62. Accademia delle Scienze di Siena detta de'Fisiocritici, Siena.
- Deharveng, L. (1980b). Contribution à la connaissance systématique, écologique et biogéographique des Collembolles Neanurinae de Corse. *Revue d'Écologie et de Biologie du Sol*, **17**, 419–35.
- Deharveng, L. (1980c). Collembolles de Papouasie Nouvelle-Guinée. 1. *Isotoma* (*Pseudisotoma*). *Nouvelle Revue d'Entomologie*, **10**, 129–32.
- Deharveng, L. (1981a). La famille des Odontellidae: phylogenèse et taxonomie. *Travaux du Laboratoire d'Écobiologie des Arthropodes Édaphiques, Toulouse*, **3**, (1), 1–21.
- Deharveng, L. (1981b). Nouvelles espèces de Neanurinae européens appartenant aux genres *Bilobella* et *Monobella*. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **117**, 95–102.
- Deharveng, L. (1981c). La chétotaxie dorsale de l'antenne et son intérêt phylogénétique chez les Collembolles Neanuridae. *Nouvelle Revue d'Entomologie*, **11**, 3–13.
- Deharveng, L. (1981d). Collembolles des îles subantarctiques de l'Océan Indien. Mission J. Travé 1972–1973. *Biologie des Sols, Comité National Français des Recherches Antarctiques*, **48**, 33–108.

- Deharveng, L. (1982a). Contribution à l'étude des Collemboles Neanurinae: évolution, spéciation, polymorphisme somatique et chromosomique des formes européennes. PhD thesis, Université Paul Sabatier, Toulouse.
- Deharveng, L. (1982b). A propos des *Folsomia* du groupe *quadrioculata* Tullberg, 1871. *Revue d'Écologie et de Biologie du Sol*, **19**, 613–27.
- Deharveng, L. (1982c). Observations préliminaires sur les collemboles cavernicoles de Papouasie (Nouvelle-Guinée). *Mémoires de Biospéologie*, **8**, 69–75.
- Deharveng, L. (1982d). Contribution à l'étude des *Deutonura* du groupe *phlegraea* (Collembola: Neanuridae). *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **3**, (2), 1–20.
- Deharveng, L. (1982e). Clé de détermination des genres de Neanurinae (Collemboles) d'Europe et de la région méditerranéenne avec description de deux nouveaux genres. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **3**, (4), 7–13.
- Deharveng, L. (1982f). Polymorphism of polytene chromosomes in *Bilobella aurantiaca* (Insecta: Collembola). Study of a population from Sierra de Gredos (Central Spain). *Chromosoma*, **85**, 201–14.
- Deharveng, L. (1982g). Contribution à la connaissance taxonomique et phylogénétique des Neanuridae. I. Le genre *Rusekella* n.g. et ses implications phylogénétiques. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **118**, 235–51.
- Deharveng, L. (1983a). Morphologie évolutive des Collemboles Neanurinae en particulier de la lignée Neanurienne. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **4**, (2), 1–63.
- Deharveng, L. (1983b). Collemboles de Papouasie (Nouvelle-Guinée). 2. *Coecoloba plumleyi* n.sp., Neanurinae cavernicole très évolué des Hautes Terres Centrales. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **119**, 59–62.
- Deharveng, L. (1984a). Un nouveau Collembole Isotomidae du Brésil: *Proisotoma oliveirae*. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **120**, 123–6.
- Deharveng, L. (1984b). Polymorphisme et polytypisme morphologiques chez quelques Neanurinae européens. *Revue d'Écologie et de Biologie du Sol*, **21**, 533–62.
- Deharveng, L. (1985). Deux remarquable espèces nouvelles du genre *Lathriopyga* Caroli, 1910 (Collembola, Neanuridae). *Nouvelle Revue d'Entomologie, N.S.*, **2**, 213–19.
- Deharveng, L. (1986a). Révision taxonomique du genre *Monobella* Cassagnau, 1979 (Collembola: Neanurinae). *Annales de la Société Entomologique de France, N.S.*, **22**, 469–89.
- Deharveng, L. (1986b). Collemboles cavernicoles. VI. Une nouvelle espèce souterraine de Neanurinae: *Deutonura mirabilis* n.sp. d'Autriche. *Bulletin de la Société Entomologique de France*, **91**, 209–11.
- Deharveng, L. (1986c). Collemboles cavernicoles. IV. Collemboles souterrains du Quercy. *Recherches sur les karsts du Quercy et du Sud-Ouest de la France, Toulouse*, pp. 79–84.
- Deharveng, L. (1986d). Collemboles. In *Expédition Thai-Maros 85. Rapport Spéléologique et Scientifique*. Association Pyréenne de Spéléologie, Toulouse. pp. 191–8.
- Deharveng, L. (1986e). Analyse phylogénétique du genre *Deutonura*. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 23–8. University of Siena, Siena.
- Deharveng, L. (1987a). Cave Collembola of South-East Asia. *Korean Journal of Systematic Zoology*, **3**, 165–74.
- Deharveng, L. (1987b). *Siamanura* n.g. nouveau genre thaïlandais de collembole Neanurinae. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **5**, (2), 1–41.
- Deharveng, L. (1987c). Révision taxonomique du genre *Tetracanthella* Schött, 1891. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **5**, (3), 1–151.
- Deharveng, L. (1987d). *Digitanura quadrilobata* gen.n. sp.n., Collembola Neanurinae de Thaïlande. *Bulletin et Annales de la Société Royale Entomologique de Belgique*, **123**, 145–51.
- Deharveng, L. (1987e). Collemboles cavernicoles et édaphiques de Sulawesi et des Moluques. In *Expédition Thai-Maros 86. Rapport Spéléologique et Scientifique*. Association Pyréenne de Spéléologie, Toulouse. pp. 133–42.
- Deharveng, L. (1988a). Collemboles Poduromorpha de Nouvelle-Calédonie. 5. Deux genres nouveaux de Neanurinae (Neanuridae). *Mémoires du Muséum National d'Histoire Naturelle*, **142A**, 45–52.
- Deharveng, L. (1988b). A new genus of neanurid Collembola from continental South-east Asia. *Canadian Journal of Zoology*, **66**, 714–19.
- Deharveng, L. (1988c). Collemboles cavernicoles. VII. *Pseudosinella bessoni* n.sp. et note sur l'évolution morphologique de la griffe chez les *Pseudosinella*. *Revue Suisse de Zoologie*, **95**, 203–8.
- Deharveng, L. (1988d). Collemboles cavernicoles. VIII. Contribution à l'étude des Oncopoduridae. *Bulletin de la Société Entomologique de France*, **92**, 133–47.
- Deharveng, L. (1988e). A new troglomorphic Collembola from Thailand: *Troglopedetes fredstonei*, new species (Collembola: Paronellidae). *Bishop Museum Occasional Papers*, **28**, 95–8.

- Deharveng, L. (1989a). Collemboles cavernicoles. IX. *Isotomiella barivierai* n.sp. et *I. unguiculata* n.sp. (Isotomidae), premiers espèces troglobies du genre *Isotomiella*. *Bulletin de la Société Entomologique de France*, **93**, 197–204.
- Deharveng, L. (1989b). The genus *Paranura* Axelson 1902 in Thailand (Collembola: Neanuridae). *Tropical Zoology*, **2**, 103–21.
- Deharveng, L. (1989c). *Caucansanura besucheti* n.sp., nouveau Neanurinae de Turquie orientale (Collembola: Neanuridae). *Revue Suisse de Zoologie*, **96**, 817–22.
- Deharveng, L. (1989d). La faune souterraine de Batu Lubang. In *Expédition Batu Karst 88. Rapport Spéléologique et Scientifique*. Association Pyrénéenne de Spéléologie, Toulouse. pp. 37–46.
- Deharveng, L. (1989e). The problem of homoplasies in Neanurinae (Insecta: Collembola): microcomputer assisted phylogeny of the genus *Deutonura*. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 183–93. University of Siena, Siena.
- Deharveng, L. (1990). Fauna of Thai caves. II. New Entomobryoidea Collembola from Chiang Dao Cave, Thailand. *Bishop Museum Occasional Papers*, **30**, 279–87.
- Deharveng, L. (1991). *Chirolavia*, a new genus of Neanurinae Collembola from Thailand with unusual antennal sensillae. *Raffles Bulletin of Zoology*, **39**, 53–8.
- Deharveng, L. and Bedos, A. (1991). Taxonomy and cladistic analysis of the Thai species of *Friesea* Dalla Torre 1895 (Collembola, Neanuridae). *Tropical Zoology*, **4**, 287–315.
- Deharveng, L. and Bedos, A. (1992). *Blasconurella*, a new genus of Neanurinae (Insecta, Collembola) from Thailand, with five new species. *Tropical Zoology*, **5**, 299–311.
- Deharveng, L. and Bedos, A. (1993a). Factors influencing diversity of soil Collembola in a tropical mountain forest (Doi Inthanon, Northern Thailand). In *Soil biota, nutrient cycling and farming systems* (ed. M.G. Paoletti, W. Foissner, and D. Coleman), pp. 91–111. Lewis, Boca Raton.
- Deharveng, L. and Bedos, A. (1993b). New *Paleonura* and *Pronura* species (Collembola, Neanurinae) from Thailand. *Zoologica Scripta*, **22**, 183–92.
- Deharveng, L. and Bedos, A. (1995). *Lepidonella lecongkietii* n.sp., premier Collembole cavernicole du Vietnam (Collembola, Paronellidae). *Bulletin de la Société Entomologique de France*, **100**, 21–4.
- Deharveng, L. and Berruete, E. (1993). *Megalothorax tuberculatus* n.sp., nouveau troglobie des Pyrénées-Atlantiques (France) et de Navarre (Espagne) (Collembola, Neelidae). *Bulletin de la Société Entomologique de France*, **98**, 15–18.
- Deharveng, L. and Bourgeois, A. (1991). Two new species of *Ceratophysella* (Collembola: Hypogastruridae) from Thailand. *Acta Zoologica Cracoviensia*, **34**, 303–10.
- Deharveng, L. and Christian, E. (1984). *Gnathofolsomia palpata* n.g., n.sp., eine Isotomide mit abgewandelten Mundwerkzeugen aus österreichischen Höhlen (Insecta, Collembola). *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich*, **122**, 97–101.
- Deharveng, L. and Diaz, A. (1984). Collemboles du Kenya. I. Liste des stations. II. Hypogastruridae. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **6A**, 335–48.
- Deharveng, L. and Fjellberg, A. (1993). *Isotomiella* from Seychelles islands (Insecta, Collembola, Isotomidae). *Spixiana*, **16**, 121–5.
- Deharveng, L. and Gers, C. (1979). Sur les genres *Xenyllogastrura* Denis, 1932 et *Orogastrura* n.g. (Collembola Hypogastruridae). *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **1**, (2), 1–10.
- Deharveng, L. and Gers, C. (1993). Ten new species of *Troglopedetes* Absolon, 1907 from caves of Thailand (Collembola, Paronellidae). *Bijdragen tot de Dierkunde*, **63**, 103–13.
- Deharveng, L. and Gouze, A. (1984). Collemboles cavernicoles. III. Sur les *Onychiurus* Français du sous-groupe *argus*. *Annales de la Société Entomologique de France*, **20**, 389–97.
- Deharveng, L. and Gouze, A. (1986). Collemboles cavernicoles. V. Une nouvelle *Pseudosinella* du gouffre de la Pierre-Saint-Martin (France; Pyrénées-Atlantiques). *Revue Suisse de Zoologie*, **93**, 215–18.
- Deharveng, L. and Greenslade, P. (1990). Species of *Australonura* (Collembola: Neanuridae) from the Solomon Islands. *Invertebrate Taxonomy*, **3**, 595–603.
- Deharveng, L. and Greenslade, P. (1992). *Hemilobella*, a new genus of Lobellini (Collembola: Neanuridae) from Australia and Malaysia with notes on other Australian Lobelline genera. *Invertebrate Taxonomy*, **6**, 727–39.
- Deharveng, L. and Leclerc, P. (1989). Recherches sur les faunes cavernicoles d'Asie du Sud-Est. *Mémoires de Biospéologie*, **16**, 91–110.
- Deharveng, L. and Lee, B.H. (1984). Polytene chromosomes variability of *Bilobella aurantiaca* (Collembola, Insecta) from St. Baume population (France). *Caryologia*, **37**, 51–67.
- Deharveng, L. and Lek, S. (1993). Remarques sur la morphologie et la taxonomie du genre *Isotomurus* Börner, 1903 et description de deux espèces nouvelles de France (Collembola: Isotomidae). *Annales de la Société Entomologique de France*, **29**, 245–59.

- Deharveng, L. and Lienhard, C. (1983). Deux nouvelles espèces du genre *Stachorutes* Dallai, 1973 (Collembola). *Revue Suisse de Zoologie*, **90**, 929–34.
- Deharveng, L. and Najt, J. (1989). Collemboles Poduromorpha de Nouvelle-Calédonie. 1. Hypogastruridae. *Mémoires du Muséum National d'Histoire Naturelle*, **142A**, 17–27.
- Deharveng, L. and Oliveira, E. (1990). *Isotomiella* (Collembola: Isotomidae) d'Amazonia: les espèces du group *delamarei*. *Annales de la Société Entomologique de France*, **26**, 185–201.
- Deharveng, L. and Oliveira, E.P. (1994). *Paracerura virgata* n.g., n.sp. (Collembola, Isotomidae), nouveau Collembola d'Amazonie centrale. *Revue Suisse de Zoologie*, **101**, 441–6.
- Deharveng, L. and Suhardjono, Y.R. (1994). *Isotomiella* Bagnall, 1939 (Collembola Isotomidae) of Sumatra (Indonesia). *Tropical Zoology*, **7**, 309–23.
- Deharveng, L. and Thibaud, J.M. (1980). Trois espèces nouvelles du genre *Schaefferia* Absolon, 1900 (Insecte, Collembola). *Nouvelle Revue d'Entomologie*, **10**, 3–10.
- Deharveng, L. and Thibaud, J.M. (1989a). Acquisitions récentes sur les Insectes Collemboles cavernicoles d'Europe. *Mémoires de Biospéologie*, **16**, 145–51.
- Deharveng, L. and Thibaud, J.M. (1989b). *Bessoniella procera* n.g. n.sp., nouvel Orchesellidae cavernicole relictuel des Pyrénées (Insecta, Collembola). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **11A**, 397–405.
- Deharveng, L. and Travé, J. (1981). Écologie des Oribates (Acariens) et des Collemboles (Insectes) de Kerguelen. *Biologie des Sols, Comité National Français des Recherches Antarctiques*, **48**, 109–41.
- Deharveng, L. and Weiner, W. (1984). Collemboles de Corée du Nord. III. Morulinae et Neanurinae. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **4**, (4), 1–61.
- Deharveng, L. and Wise, K.A.J. (1987). A new genus of Collembola (Neanuridae: Neanurinae) from southern New Zealand. *Record of the Auckland Institute and Museum*, **24**, 143–6.
- Deharveng, L., Bedos, A., and Leksawadi, P. (1989). Diversity in tropical forest soils: the Collembola of Doi Inthanon (Thailand). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 317–28. University of Siena, Siena.
- Dejean, A. (1985). An ecoethological study of predation in the ant genus *Sminthistruma* (Formicidae, Myrmicinae, Dacetini). 2. Attraction of the principal prey (Collembola). *Insectes Sociaux*, **32**, 158–72.
- Dekkers, T.B.M., Van der Werff, P.A., and Van Amelsvoort, P.A.M. (1994). Soil Collembola and Acari related to farming systems and crop rotations in organic farming. *Acta Zoologica Fennica*, **195**, 28–31.
- Delamare Deboutteville, C. (1964). Documents pour une histoire des Insectes Collemboles. Première note: le genre *Actaletes* Giard. *Revue d'Écologie et de Biologie du Sol*, **1**, 413–19.
- Delamare Deboutteville, C. and Massoud, Z. (1964a). Le genre *Vesicephalus* Richards de la sous-famille des Vesicephalinae Richards nov.comb., avec une discussion de la position du genre *Papirinus* Yosii (Ins. Collembola Symphyleona). *Revue d'Écologie et de Biologie du Sol*, **1**, 73–83.
- Delamare Deboutteville, C. and Massoud, Z. (1964b). *Collophora remanei* n.ssp., Collembola Symphyléone du Pérou et remarques sur le genre *Collophora* Richards et sa position systématique. *Zoologischer Anzeiger*, **172**, 30–6.
- Delamare Deboutteville, C. and Massoud, Z. (1964c). Collemboles Symphyléones du Surinam. *Studies on the Fauna of Suriname and other Guyanas*, **26**, 56–81.
- Delamare Deboutteville, C. and Massoud, Z. (1967). Une groupe panchronique: les Collemboles essai critique sur *Rhyniella praecursor*. *Annales de la Société Entomologique de France, N.S.*, **3**, 625–9.
- Delamare Deboutteville, C. and Massoud, Z. (1968). Révision de *Protentomobrya walkeri* Folsom, Collembola du Crétacé, et remarques sur sa position systématique. *Revue d'Écologie et de Biologie du Sol*, **4**, 619–30.
- Desender, K., Mertens, J., Dhulster, M., and Berbiere, P. (1984). Diel activity patterns of Carabidae (Coleoptera), Staphylinidae (Coleoptera) and Collembola in a heavily grazed pasture. *Revue d'Écologie et de Biologie du Sol*, **21**, 347–61.
- Diaz, A. and Najt, J. (1983). Un nouveau genre de collembola Hypogastruridae de Venezuela. *Nouvelle Revue d'Entomologie*, **13**, 29–32.
- Diaz, A. and Najt, J. (1994). Collemboles (Insecta) des Andes vénézuéliennes. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **16A**, 417–35.
- Diaz, A. and Palacios-Vargas, J.G. (1983). Contribucion a la taxonomia del genero *Schoettella* (Collembola: Hypogastruridae) con descripcion de una nueva especie de Venezuela. *Caribbean Journal of Science*, **19**, 81–91.
- Didden, W.A.M. (1987). Reactions of *Onychiurus fimatus* (Collembola) to loose and compact soil. Methods and first results. *Pedobiologia*, **30**, 93–100.
- Diekkrüger, B. and Röske, H. (1995). Modelling the population dynamics of *Isotoma notabilis* (Collembola) on sites of different agricultural usage. *Pedobiologia*, **39**, 58–73.

- Disney, R.H.L. (1983). A synopsis of the taxonomist's tasks, with particular attention to phylogenetic cladism. *Field Studies*, **5**, 841–65.
- Disney, R.H. (1994). Defending cladistics. *Antenna*, **18**, 108–9.
- Doering, D. (1986). On the male reproduction biology of *Orchesella cincta* (Collembola, Entomobryidae). In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 171–6. University of Siena, Siena.
- Dohle, W. (1988). *Myriapoda and the ancestry of insects*. Manchester Polytechnic, Manchester.
- Dorel, F.G. and Verhoef, H.A. (1987). Effects of Collembola on the nitrogen mineralization in coniferous forests with and without nitrogen deposition. *Netherlands Journal of Zoology*, **37**, 430.
- Draheim, R. and Larink, O. (1995). Effects of differently cultured fungi as a diet of Collembola. *Acta Zoologica Fennica*, **196**, 168–70.
- Dunger, W. (1972). Systematische und ökologische Studien an der Apterygoten-fauna des Neißetales bei Ostritz/Oberlausitz. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **47**, (4), 1–44.
- Dunger, W. (1976a). Taxonomische Beiträge zur Unterfamilie Onychiurinae Bagnall 1935 (Collembola). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **50**, (5), 1–16.
- Dunger, W. (1976b). Strukturelle Untersuchungen an Collembolengemeinschaften des Hruby Jeseník-Gebirges (Altwatergebirge, CSSR). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **50**, (6), 1–44.
- Dunger, W. (1978a). Poduromorphe Collembolen (Insecta, Collembola) aus der Mongolischen Volksrepublik. I. Onychiuridae. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **52**, (6), 1–20.
- Dunger, W. (1978b). Bodenzologische Untersuchungen an rekultivierten Kippböden der Niederlausitz. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **52**, (11), 1–19.
- Dunger, W. (1982). Collembolen (Insecta, Collembola) aus der Mongolischen Volksrepublik. II. Isotomidae. *Annales Historico-Naturales Musei Nationalis Hungarici*, **74**, 35–74.
- Dunger, W. (1983). Collembolen (Insecta, Collembola) aus der Mongolischen Volksrepublik. III. Poduridae, Hypogastruridae und Neanuridae. *Annales Historico-Naturales Musei Nationalis Hungarici*, **75**, 121–37.
- Dunger, W. (1986). Observations on the ecological behaviour on some species of the *Tullbergia krausbaueri* group. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 111–15. University of Siena, Siena.
- Dunger, W. (1987). *Proisotoma topsenti* Denis, 1948, eine seltene, übervermehrung neigende Art der Collembola (Insecta). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **60**, (12), 53–60.
- Dunger, W. (1991a). Long term studies on soil fauna at woodland sites with increasing industrial pollution. *Revue d'Écologie et de Biologie du Sol*, **28**, 31–9.
- Dunger, W. (1991b). Ökologische Prüfung von Morphospecies der 'Tullbergia krausbaueri Gruppe' (Insecta: Collembola). *Mitteilungen aus dem Zoologischen Museum in Berlin*, **67**, 131–40.
- Dunger, W. (1991c). *Folsomia bogojevicae* n.sp., eine neue Art der Collembola (Insecta) aus Serbien. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **65**, (7), 11–15.
- Dunger, W. and Brefeld, G. (1989). Zwei neue Arten der Gattung *Sphaeridia* Linnaniemi, 1912 aus Europa (Insecta, Collembola). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **62**, (4), 1–15.
- Dunger, W. and Fritzlar, F. (1986). *Sminthurides bifidus* Mills, 1934 (Collembola, Insecta) in Europa eingeschleppt. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **59**, (9), 47–50.
- Dunger, W. and Schultz, H.J. (1989). Studies on the settlement of *Sphagnum* bogs in a heath bog by Collembola. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 355–61. University of Siena, Siena.
- Dunger, W. and Zivadinovic, J. (1983). A new European species of *Triacanthella* Schäffer, 1897 (Collembola, Hypogastruridae). *Revue d'Écologie et de Biologie du Sol*, **20**, 589–95.
- Dunger, W. and Zivadinovic, J. (1989). Taxonomie und Verbreitung der Gattung *Folsomia* Willem 1902 (Hexapoda, Collembola) in Bosnien und Hercegovina (Jugoslawien). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **63**, (4), 1–12.
- Edwards, C.A. (1962). Springtail damage to bean seedlings. *Plant Pathology*, **11**, 67–8.
- Edwards, C.A. (1969). Effects of gamma irradiation on populations of soil invertebrates. In *Proceedings of the Second Symposium on Radioecology*, Ann Arbor, Michigan. U.S., pp. 68–77. Atomic Energy Commission, Tennessee.
- Edwards, C.A. (1991). The assessment of populations of soil-inhabiting invertebrates. *Agriculture, Ecosystems and Environment*, **34**, 145–76.
- Edwards, C.A., Dennis, E.B., and Empson, P.W. (1967). Pesticides and the soil fauna: effects of aldrin and DDT in an arable field. *Annals of Applied Biology*, **60**, 11–22.
- Edwards, D. and Selden, P.A. (1992). The development of early terrestrial ecosystems. *Botanical Journal of Scotland*, **46**, 337–66.

- Edwards, D., Selden, P.A., Richardson, J.B., and Axe, L. (1995). Coprolites as evidence for plant-animal interaction in Siluro-Devonian terrestrial ecosystems. *Nature*, **377**, 329–31.
- Eijsackers, H. (1975). Effects of the herbicide 2,4,5-T on *Onychiurus quadricellatus* Gisin (Coll.). In *Progress in soil zoology* (ed. J. Vanek), pp. 481–8. Academia, Prague.
- Eijsackers, H. (1978a). Side effects of the herbicide 2,4,5-T on reproduction, food consumption and moulting of the springtail *Onychiurus quadricellatus* Gisin (Collembola). *Zeitschrift für Angewandte Entomologie*, **85**, 341–60.
- Eijsackers, H. (1978b). Side effects of the herbicide 2,4,5-T affecting mobility and mortality of the springtail *Onychiurus quadricellatus* Gisin (Collembola). *Zeitschrift für Angewandte Entomologie*, **86**, 349–72.
- Eisenbeis, G. (1974). Licht- und elektronenmikroskopische Untersuchungen zur Ultrastruktur des Transportepithels am Ventraltubus arthropleoner Collembolen (Insecta). *Cytobiologie*, **9**, 180–202.
- Eisenbeis, G. (1976a). Zur Morphologie des Ventraltubus von *Tomocerus* ssp. (Collembola: Tomoceridae) unter besonderer Berücksichtigung der Muskulatur, der cuticularen Strukturen und der Ventralrinne. *International Journal of Insect Morphology and Embryology*, **5**, 357–79.
- Eisenbeis, G. (1976b). Zur Feinstruktur und Funktion von Sensillen im Transport-Epithel des Ventraltubus von *Tomocerus* und *Orchesella* (Collembola: Tomoceridae/Entomobryidae). *Entomologica Germanica*, **2**, 271–95.
- Eisenbeis, G. (1978). Die Thorakal- und Abdominal-Muskulatur von Arten der Springschwanz-Gattung *Tomocerus* (Collembola: Tomoceridae). *Entomologica Germanica*, **4**, 55–83.
- Eisenbeis, G. (1982). Physiological absorption of liquid water by Collembola: absorption by the ventral tube at different salinities. *Journal of Insect Physiology*, **28**, 11–20.
- Eisenbeis, G. (1989a). Allometric relationships of the body surface area to body mass in different life forms of soil arthropods. 1. Comparative investigations of surface constants and allometric components. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 371–85. University of Siena, Siena.
- Eisenbeis, G. (1989b). Allometric relationships of the body surface area to body mass in different life forms of soil arthropods. 2. Surface area and climate. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 387–400. University of Siena, Siena.
- Eisenbeis, G. (1994). Die Biologische Aktivität von Böden aus zoologischer Sicht. *Braunschweig Naturkd. Schr.*, **4**, 653–8.
- Eisenbeis, G. and Meyer, E. (1986). Some ultrastructural features of glacier Collembola *Isotoma* 'sp. g' and *Isotomurus palliceps* (Uzel, 1891) from the Tyrolean Central Alps. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 257–72. University of Siena, Siena.
- Eisenbeis, G. and Ulmer, S. (1978). Zur Funktionsmorphologie des Sprung-Apparates der Springschwänze am Beispiel von Arten der Gattung *Tomocerus* (Collembola: Tomoceridae). *Entomologia Generalis*, **5**, 35–55.
- Eisenbeis, G. and Wichard, W. (1975a). Histochemischer Chloridnachweis im Transportepithel am Ventraltubus arthropleoner Collembolen. *Journal of Insect Physiology*, **21**, 231–6.
- Eisenbeis, G. and Wichard, W. (1975b). Feinstruktureller und histochemischer Nachweis des Transportepithels am Ventraltubus symphypleoner Collembolen (Insecta, Collembola). *Zeitschrift für Morphologie der Tiere*, **81**, 103–10.
- Eisenbeis, G. and Wichard, W. (1977). Zur feinstrukturellen Anpassung des Transportepithels am Ventraltubus von Collembolen bei unterschiedlicher Salinität. *Zoomorphologie*, **88**, 175–88.
- Eisenbeis, G. and Wichard, W. (1987). *Atlas on the biology of soil arthropods*. Springer Verlag, Berlin, Heidelberg.
- Elbourne, C.A. (1970). Influences of substrate and structure on the colonisation of an artifact-simulating decaying oak-wood on oak trunks. *Oikos*, **21**, 32–41.
- Ellis, W.N. (1967). Studies on neotropical Collembola. I. Some Collembola from Guatemala. *Beaufortia*, **14**, 93–107.
- Ellis, W.N. (1970). *Proisotoma filifera* Denis in Holland, with a note on its classification (Collembola, Isotomidae). *Entomologische Berichten*, **30**, 18–24.
- Ellis, W.N. (1973). Oecologie van epigeïsche Collembola in Voornes Duin. *De Levende Natuur*, **76**, 191–9.
- Ellis, W.N. (1974a). The spring fauna of Collembola (Insecta) from Rhodos, with description of some new taxa. *Beaufortia*, **22**, 105–52.
- Ellis, W.N. (1974b). Ecology of epigeic Collembola in the Netherlands. *Pedobiologia*, **14**, 232–7.
- Ellis, W.N. (1974c). Some Collembola from Ibiza with descriptions of three new species, and a note on *Hypogastrura serrata* (Ågren, 1904). *Bulletin Zoologisch Museum, Universiteit van Amsterdam*, **3**, 125–41.
- Ellis, W.N. (1975). On *Bourletiella* (*Cassagnaudiella*) *pruinosa* (Tullberg, 1871) and its allies (Collembola: Sminthuridae). *Bulletin Zoologisch Museum, Universiteit van Amsterdam*, **4**, 69–81.

- Ellis, W.N. (1976). Autumn fauna of Collembola from central Crete. *Tijdschrift voor Entomologie*, **119**, 221–326.
- Ellis, W.N. and Bellinger, P.F. (1973). An annotated list of generic names of Collembola (Insecta) and their type species. *Monografieën Nederlandse Entomologische Vereniging*, **7**, 1–74.
- Ellis, W.N. and Bellinger, P.F. (1984). Generic names of Collembola: Supplement 1973–1983. *Tijdschrift voor Entomologie*, **127**, 1–15.
- Ernsting, G. and Fokkema, D.S. (1983). Antennal damage and regeneration in springtails (Collembola) in relation to predation. *Netherlands Journal of Zoology*, **33**, 476–84.
- Ernsting, G. and Jansen, W. (1978). Interspecific and intraspecific selection by the predator *Notiophilus biguttatus* F. (Carabidae) concerning two collembolan prey species. *Oecologia*, **33**, 173–83.
- Ernsting, G. and Joosse, E.N.G. (1975). Predation on two species of surface dwelling Collembola. A study with radio-isotope labelled prey. *Pedobiologia*, **14**, 222–31.
- Ernsting, G., Zonneveld, C., Isaaks, J.A., and Kroon, A. (1993). Size at maturity and patterns of growth and reproduction in an insect with indeterminate growth. *Oikos*, **66**, 17–26.
- Evans, M.E.G. and Forsythe, T.G. (1985). Feeding mechanisms, and their variation in form, of some adult ground-beetles (Coleoptera: Caraboidea). *Journal of Zoology*, **206**, 113–43.
- Faber, J.H. (1991a). Functional classification of soil fauna: a new approach. *Oikos*, **62**, 110–17.
- Faber, J.H. (1991b). The interaction of Collembola and mycorrhizal roots in nitrogen mobilization in a Scots pine forest soil. In *Advances in management and conservation of soil fauna* (ed. G.K. Veeresh, D. Rajagopal, and C.A. Viraktamath), pp. 507–15. Oxford and IBH, New Delhi.
- Faber, J.H. and Joosse, E.N.G. (1993). Vertical distribution of Collembola in a *Pinus nigra* organic soil. *Pedobiologia*, **37**, 336–50.
- Faber, J.H. and Verhoef, H.A. (1991). Functional differences between closely-related soil arthropods with respect to decomposition processes in the presence or absence of pine tree roots. *Soil Biology and Biochemistry*, **23**, 15–23.
- Faber, J.H., Teuben, A., Berg, M.P., and Doelman, P. (1992). Microbial biomass and activity in pine litter in the presence of *Tomocerus minor* (Insecta, Collembola). *Biology and Fertility of Soils*, **12**, 233–40.
- Fabian, M. and Petersen, H. (1994). Short-term effects of the insecticide dimethoate on activity and spatial distribution of a soil-inhabiting collembolan *Folsomia fimetaria* Linné (Collembola: Isotomidae). *Pedobiologia*, **38**, 289–302.
- Fanciulli, P.P., Dallai, R., and Petrucci, R. (1985). A preliminary study on enzyme diversity in *Tetrodontophora bielanensis* (Waga) (Insecta, Collembola). *Revue d'Écologie et de Biologie du Sol*, **22**, 483–95.
- Fanciulli, P.P., Dallai, R., and Petrucci, R. (1986a). Enzymatic polymorphism in geographically isolated populations of *Thaumanura ruffoi*. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 197–202. University of Siena, Siena.
- Fanciulli, P.P., Dallai, R., and Petrucci, R. (1986b). Chromosomal and isozymic analysis in three populations of *Lathriopyga longiseta*. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 203–10. University of Siena, Siena.
- Fanciulli, P.P., Dallai, R., and Frati, F. (1989). Different karyotypes in *Lathriopyga longiseta*. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 157–66. University of Siena, Siena.
- Fanciulli, P.P., Frati, F., Dallai, R., and Rusek, J. (1991a). High genetic diversity among populations of *Tetrodontophora bielanensis* (Insecta, Collembola) in Europe. *Revue d'Écologie et de Biologie du Sol*, **28**, 165–73.
- Fanciulli, P.P., Frati, F., and Dallai, R. (1991b). The polytene chromosomes of *Cansilianura malatestai* (Insecta, Collembola). *Caryologia*, **44**, 11–20.
- Fanciulli, P.P., Frati, F., Carapelli, A., and Dallai, R. (1994). Livelli di variabilità e flusso genico specie del genere *Allacma* (Collembola: Sminthuridae). *Atti del XVII Congresso Nazionale Italiano di Entomologia*, pp. 73–76. Bertelli and Piccardi, Firenze.
- Ferard, M. and Poinot-Balaguer, N. (1989). Influence du type de nourriture sur les spectres esteraseiques du Collembol *Folsomia candida* W. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 457–66. University of Siena, Siena.
- Farrow, R.A. and Greenslade, P. (1992). A vertical migration of Collembola. *Entomologist*, **111**, 38–45.
- Filser, J. (1990). Halbfreilandversuch zur Auswirkung des Insektizids endosulphan auf Collembolen. *Verhandlungen der Gesellschaft für Ökologie*, **19**, 302–9.
- Filser, J. (1991). Sommer- und Wintergesellschaften der epigäischen Collembolen in Hopfengärten unterschiedlicher Bewirtschaftung. *Verhandlungen der Gesellschaft für Ökologie*, **20**, 55–9.
- Filser, J. (1994). The effect of the systemic fungicide Aktuan on Collembola under field conditions. *Acta Zoologica Fennica*, **195**, 32–4.

- Filser, J. (1995a). Collembola as indicators for long-term effects of intensive management. *Acta Zoologica Fennica*, **196**, 326–8.
- Filser, J. (1995b). The effects of green manure on the distribution of Collembola in a permanent row crop. *Biology and Fertility of Soils*, **19**, 303–8.
- Filser, J. and Fromm, H. (1995). The vertical distribution of Collembola in an agricultural landscape. *Polskie Pismo Entomologiczne*, **64**, 99–112.
- Filser, J. and Nagel, R.F. (1993). Untersuchungen zur Vergleichbarkeit von Insektizideffekten auf Collembolen unter Labor- und Freilandbedingungen. *Verhandlungen der Gesellschaft für Ökologie*, **22**, 397–402.
- Filser, J., Fromm, H., Nagel, R.F., and Winter, K. (1995). Effects of previous intensive agricultural management on microorganisms and the biodiversity of soil fauna. *Plant and Soil*, **170**, 123–9.
- Finlay, R.D. (1985). Interactions between soil micro-arthropods and endomycorrhizal associations of higher plants. In *Ecological interactions in soil: plants, microbes and animals* (ed. A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher) pp. 319–31. Blackwell, Oxford.
- Fjellberg, A. (1973a). New records for *Vertagopus sarakensis* (Wahlgren, 1906) from Northern Scandinavia (Collembola, Isotomidae). *Entomologica Scandinavica*, **4**, 241–8.
- Fjellberg, A. (1973b). Observations of *Onychiurus nervosus* Stach, 1954 (Collembola, Onychiuridae) in Eastern Norway. *Norsk Entomologisk Tidsskrift*, **20**, 263–5.
- Fjellberg, A. (1973c). Some morphological differences between *Proisotoma minuta* (Tullberg, 1871) and *P. clavipila* (Axelson, 1903) (Collembola, Isotomidae). *Norsk Entomologisk Tidsskrift*, **20**, 273–4.
- Fjellberg, A. (1973d). *Anurida frigida*. A new species of Collembola (Hypogastruridae) from Swedish Lappland. *Norsk Entomologisk Tidsskrift*, **20**, 285–7.
- Fjellberg, A. (1974a). *Karlstejnina norvegica*. A new species of Collembola (Onychiuridae, Tullberginae) from the alpine regions in Southern Norway. *Norsk Entomologisk Tidsskrift*, **21**, 15–18.
- Fjellberg, A. (1974b). *Anurophorus atlanticus* n.sp. A new species of Collembola (Isotomidae) from Western Norway. *Norsk Entomologisk Tidsskrift*, **21**, 127–30.
- Fjellberg, A. (1974c). *Spinosellina* forms of *Sminthurides schoetti* (Axelson) and *S. parvulus* (Krausbauer) (Collembola) in Norway. *Norsk Entomologisk Tidsskrift*, **21**, 185–6.
- Fjellberg, A. (1975a). Organization and dynamics of Collembola populations on Hardangervidda. In *Ecological studies. Analysis and synthesis*, Vol. 17, *Fennoscandian Tundra Ecosystems*, Part 2. (ed. F.E. Wielgolaski), pp. 73–9. Springer-Verlag, Berlin, Heidelberg.
- Fjellberg, A. (1975b). Redescrptions of some little known Collembola from Scandinavia (Insecta: Collembola). *Entomologica Scandinavica*, **6**, 81–8.
- Fjellberg, A. (1975c). *Vertagopus pseudocinereus* n.sp. A new species of Collembola (Isotomidae) from North Norway. *Entomologica Scandinavica*, **6**, 212–14.
- Fjellberg, A. (1976a). Cyclomorphosis in *Isotoma hiemalis* Schött, 1893 (*mucronata* Axelson, 1900) syn.nov. (Collembola, Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **13**, 381–4.
- Fjellberg, A. (1976b). An anomalous specimen of *Proisotoma subantarctica* Gisin with traces of appendages on the second abdominal segment (Collembola, Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **13**, 517–19.
- Fjellberg, A. (1976c). *Proisotoma armeriae* n.sp. A new species of Collembola (Isotomidae) from West Norway. *Entomologica Scandinavica*, **7**, 233–5.
- Fjellberg, A. (1976d). Problems and methods in current research on Collembola systematics. *Zoologica Scripta*, **5**, 167–9.
- Fjellberg, A. (1976e). Collembola from mountains in South Norway. *Norwegian Journal of Entomology*, **23**, 127–37.
- Fjellberg, A. (1976f). Mire invertebrate fauna at Eidskog, Norway. II. Surface-active Collembola. *Norwegian Journal of Entomology*, **23**, 181–3.
- Fjellberg, A. (1977a). Epitoky in *Vertagopus* species (Collembola, Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **14**, 493–5.
- Fjellberg, A. (1977b). On the identity of *Isotoma ekmani* nom.nov. pro *I. pallida* Agrell, 1939 (nec Nicolet, 1842, Moniez, 1894) (Collembola: Isotomidae). *Entomologica Scandinavica*, **8**, 9–11.
- Fjellberg, A. (1978a). Generic switch-over in *Isotoma nivea* Schäffer, 1896. A new case of cyclomorphosis in Collembola (Isotomidae). *Norwegian Journal of Entomology*, **25**, 221–2.
- Fjellberg, A. (1978b). New species of the genus *Isotoma* Bourlet, 1839 from North America (Collembola: Isotomidae). *Entomologica Scandinavica*, **9**, 93–110.
- Fjellberg, A. (1979). Revision of the European species in the *Isotoma olivacea* group (Collembola: Isotomidae). *Entomologica Scandinavica*, **10**, 91–108.
- Fjellberg, A. (1980a). *Identification keys to Norwegian Collembola*. Norsk Entomologisk Forening, Ås-NLH.

- Fjellberg, A. (1980b). *Archisotoma theae* n.sp. from Norway, with notes on some systematic important characters of the genus (Collembola: Isotomidae). *Entomologica Scandinavica*, **11**, 154–8.
- Fjellberg, A. (1980c). Redescriptions of *Vertagopus brevicaudus* (Carpenter, 1900) and *V. reuteri* (Schött, 1893), two arctic species of Collembola (Isotomidae). *Entomologica Scandinavica*, **13**, 141–7.
- Fjellberg, A. (1984a). Collembola from Jan Mayen, Bjørnøya and Hopen with additions to the species list from Spitsbergen. *Fauna Norvegica*, **31B**, 69–76.
- Fjellberg, A. (1984b). The maxillary outer lobe, an important systematic tool in Isotomidae (Collembola). *Annales de la Société Royale Zoologique de Belgique*, **114**, 83–8.
- Fjellberg, A. (1984c). Maxillary structures in Hypogastruridae (Collembola). *Annales de la Société Royale Zoologique de Belgique*, **114**, 89–99.
- Fjellberg, A. (1984d). Collembola from the Colorado Front range, U.S.A. *Arctic and Alpine Research*, **16**, 193–208.
- Fjellberg, A. (1985a). Recent advances and future needs in the study of Collembola biology and systematics. *Quaestiones Entomologicae*, **21**, 559–70.
- Fjellberg, A. (1985b). Arctic Collembola. I. Alaskan Collembola of the families Poduridae, Hypogastruridae, Odontellidae, Brachystomellidae and Neanuridae. *Entomologica Scandinavica*, Supplement, **21**, 1–126.
- Fjellberg, A. (1985c). Elements of dorsal chaetotaxy in Neanuridae with descriptions of two new species of *Anurida* (Collembola). *Entomologica Scandinavica*, **15**, 349–62.
- Fjellberg, A. (1985d). *Xenyllodes wapiti* sp.n., a new species of Collembola (Odontellidae) from western Canada. *Entomologica Scandinavica*, **16**, 131–3.
- Fjellberg, A. (1986a). *The systematics and distribution of Collembola in the Northern Holarctic region*. PhD thesis, University of Tromsø.
- Fjellberg, A. (1986b). Collembola of the Canadian High Arctic. Review and additional records. *Canadian Journal of Zoology*, **64**, 2386–90.
- Fjellberg, A. (1986c). Revision of the genus *Agrenia* Börner, 1906 (Collembola: Isotomidae). *Entomologica Scandinavica*, **17**, 93–106.
- Fjellberg, A. (1987a). Northern species of *Onychiurus* Gervais, 1841, subgenus *Archaphorura* Bagnall, 1949 (Collembola: Onychiuridae). *Entomologica Scandinavica*, **18**, 279–88.
- Fjellberg, A. (1987b). A new species of *Hypogastrura* (*Mucrella*) from Indiana, USA (Collembola, Hypogastruridae). *Entomologica Scandinavica*, **18**, 289–91.
- Fjellberg, A. (1988a). The collembole fauna of Troms and Finnmark, North Norway (Collembola). *Fauna Norvegica*, **35B**, 5–20.
- Fjellberg, A. (1988b). Six new species of Collembola from North Norway (Hypogastruridae, Odontellidae, Onychiuridae, Isotomidae). *Fauna Norvegica*, **35B**, 35–41.
- Fjellberg, A. (1988c). *Proisotoma rainieri* Folsom, 1937 (= *Isotoma kisoana* Yosii, 1939) syn.nov. An epitokous species of Collembola (Isotomidae). *Canadian Journal of Zoology*, **66**, 965–7.
- Fjellberg, A. (1988d). *Agrenia lamellosa*, a new species of Collembola (Isotomidae) from Pennsylvania. *Journal of the New York Entomological Society*, **96**, 110–12.
- Fjellberg, A. (1989). Redescription of *Mackenziella psocoides* Hammer, 1953 and discussion of its systematic position (Collembola, Mackenziellidae). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 93–105. University of Siena, Siena.
- Fjellberg, A. (1991a). *Proisotoma roberti* n.sp. from Greenland, and redescription of *P. ripicola* Linnaniemi, 1912 (Collembola, Isotomidae). *Entomologiske Meddelelser*, **59**, 81–3.
- Fjellberg, A. (1991b). Rediscovery of *Knowltonella idahoensis* Wray, an autapomorphous *Schoettella* Schäffer (Collembola: Hypogastruridae). *Entomologica Scandinavica*, **21**, 427–9.
- Fjellberg, A. (1991c). Tibiotarsal chaetotaxy in Tullbergiinae (Collembola: Onychiuridae). *Entomologica Scandinavica*, **21**, 431–4.
- Fjellberg, A. (1991d). Tibiotarsal chaetotaxy in *Willemia* Börner, with description of a new species from North America (Collembola: Hypogastruridae). *Entomologica Scandinavica*, **22**, 205–7.
- Fjellberg, A. (1991e). Collembola of the Canary Islands. I. Introduction and survey of the family Hypogastruridae. *Entomologica Scandinavica*, **22**, 437–56.
- Fjellberg, A. (1992a). *Hypogastrura* (*Mucrella*) *arborea* sp.nov., a tree-climbing species of Collembola (Hypogastruridae) from Vancouver Island, British Columbia. *Canadian Entomologist*, **124**, 405–7.
- Fjellberg, A. (1992b). Revision of European and North African *Folsomides* Stach with special emphasis on the Canadian fauna (Collembola: Isotomidae). *Entomologica Scandinavica*, **23**, 453–73.
- Fjellberg, A. (1994). *The Collembola of the Norwegian Arctic Islands*. Meddelelser Nr. 133, Norsk Polarinstitutt, Oslo.
- Fjellberg, A. (1995a). Collembola of the Canary Islands. II. Family Odontellidae. *Entomologica Scandinavica*, **26**, 152–8.

- Fjellberg, A. (1995b). The systematic position of the monotypic family Isotogastruridae (Collembola) with description of *Isotogastrura coronata* n.sp. from Fuerteventura, Canary Islands. *Miscelanea Zoologica*, **17**, 123–7.
- Fjellberg, A. and Poinso, N. (1975). *Archisotoma polaris* n.sp. A new species of Collembola (Isotomidae) from Spitsbergen. *Norwegian Journal of Entomology*, **22**, 109–12.
- Fodde, R., Petrucci, R., Fanciulli, P.P., Bernini, L., and Dallai, R. (1986). Cross hybridization of a human cDNA sequence with genomic DNA from *Thaumanura ruffoi*. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 193–6. University of Siena, Siena.
- Folsom, J.W. (1902). Collembola of the grave. *Psyche*, **9**, 363–7.
- Folsom, J.W. (1937). Nearctic Collembola or springtails of the family Isotomidae. *Proceedings of the United States National Museum*, **168**, 1–144.
- Ford, J. (1935). The animal population of a meadow near Oxford. *Journal of Animal Ecology*, **4**, 195–207.
- Forey, P.L., Humphries, C.J., Kitching, I.J., Scotland, R.W., Siebert, D.J., and Williams, D.M. (1992). *Cladistics: a practical course in systematics*. Oxford University Press.
- Foster, G.N. (1970). Natural enemies of *Bourletiella hortensis* (Fitch) (Collembola). *Entomologist's Monthly Magazine*, **106**, 96.
- Fox, A.D. and Stroud, D.A. (1986). Diurnal rhythms in a snow-surface springtail (*Isotoma violacea*, Collembola) and its predators in Eqaungmiut Nunaat, West Greenland. *Pedobiologia*, **29**, 405–12.
- Frampton, G.K. (1988a). The effects of some commonly-used foliar fungicides on Collembola in winter barley: laboratory and field studies. *Annals of Applied Biology*, **113**, 1–14.
- Frampton, G.K. (1988b). Effects of the foliar fungicide pyrazophos on cereal Collembola. In *Environmental effects of pesticides*. BCPC Monograph No. 40, pp. 319–26.
- Frampton, G.K. (1994). Sampling to detect effects of pesticides on epigeal Collembola. *Aspects of Applied Biology*, **37**, 121–30.
- Frampton, G.K., Langton, S.D., Greig-Smith, P.W., and Hardy, A.R. (1992). Changes in the soil fauna at Boxworth. In *Pesticides, cereal farming and the environment: the Boxworth project* (ed. P. Greig-Smith, G.K. Frampton, and T. Hardy), pp. 132–43. HMSO, London.
- François, J. and Chaudonneret, J. (1982). Les formations endosquelettiques céphaliques des collembolles et autres aptérygotes. *Bulletin de la Société Zoologique de France*, **107**, 537–43.
- Frati, F. and Szeptycki, A. (1990). Two new species of *Orchesella* Templeton, 1835 (Collembola, Entomobryidae) from central Italy. *Redia*, **73**, 283–91.
- Fratello, B., Bertolani, R., Sabatini, M.A., Mola, L., and Rassa, M.A. (1985). Effects of atrazine on soil microarthropods in experimental maize fields. *Pedobiologia*, **28**, 161–8.
- Fratello, B., Bertolani, R., Sabatini, M.A., and Mola, L. (1986). Effects of the herbicide atrazine on Collembola. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 143–8. University of Siena, Siena.
- Frati, F., Fanciulli, P.P., and Dallai, R. (1989). Biochemical approach to the systematics of Collembola. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 145–55. University of Siena, Siena.
- Frati, F., Fanciulli, P.P., and Dallai, R. (1991). Diversità genetica nei Collemboli. *Atti del XVI Congresso Nazionale Italiano di Entomologia*, pp. 877–83. Bertelli and Piccardi, Firenze.
- Frati, F., Fanciulli, P.P., and Posthuma, L. (1992a). Allozyme variation in reference and metal-exposed natural populations of *Orchesella cincta* (Insecta, Collembola). *Biochemical Systematics and Ecology*, **20**, 297–310.
- Frati, F., Fanciulli, P.P., and Dallai, R. (1992b). Genetic diversity and taxonomy in soil-dwelling insects: the genus *Orchesella*. *Journal of Heredity*, **83**, 275–81.
- Frati, F., Fanciulli, P.P., and Dallai, R. (1994). Further acquisitions on systematics relationships within the genus *Orchesella* (Collembola, Entomobryidae) using allozymes. *Acta Zoologica Fennica*, **195**, 35–43.
- Freeman, J.A. (1952). Occurrence of Collembola in the air. *Proceedings of the Royal Entomological Society of London*, **27A**, 28.
- Friedrich, M. and Tautz, D. (1995). Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. *Nature*, **376**, 165–7.
- Fritsch, N. (1992). Collembolen sin Stammbaufbereich von Buchen. Untersuchungsfläche Bliesmengen-Bolchen/Bliesgau. *Faunistisch-Floristische Notizen aus dem Saarland*, **24**, 225–48.
- Fritzlär, F., Dunger, W., and Schäller, G. (1986). Über den Einfluß von Luftverunreinigungen auf Ökosysteme. X. Collembola im Immissionsgebiet eines Phosphat-Düngemittelwerkes. *Pedobiologia*, **29**, 413–14.
- Fromm, H. and Filsler, J. (1991). Modellversuch zur Endosulfanwirkung auf Collembolen und Mikroorganismen. *Verhandlungen der Gesellschaft für Ökologie*, **20**, 61–4.
- Fryc, W. (1971). Histochemical analysis of early developmental stages of *Tetradontophora bielensis* (Waga) (Collembola). Lipids. *Zeszyty Naukowe Uniwersytetu Jagiellońskiego, Prace Zoologiczne*, **267**, (17), 39–46.

- Gama, M.M. da (1961a). Nouvelle contribution pour l'étude des Collemboles du Portugal Continental. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra*, **269**, 1–43.
- Gama, M.M. da (1961b). Nova contribuição para o estudo dos Colêmbolas da Ilha da Madeira. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra*, **274**, 1–20.
- Gama, M.M. da (1963). Monografia do género *Isotomodes*. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra*, **284**, 1–44.
- Gama, M.M. da (1964). Colêmbolos de Portugal Continental. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra*, **292**, 1–252.
- Gama, M.M. da (1966). Cinq espèces nouvelles du genre *Xenylla* trouvées en Angola. *Publicações Culturais Companhia de Diamantes de Angola*, **72**, 123–34.
- Gama, M.M. da (1969). Notes taxonomiques et lignées généalogiques de quarante deux espèces et sous-espèces du genre *Xenylla*. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra*, **308**, 1–61.
- Gama, M.M. da (1971a). Application de la méthode de la 'systematique idéale' à quelques espèces du genre *Xenylla*. *Revue d'Écologie et de Biologie du Sol*, **8**, 189–93.
- Gama, M.M. da (1971b). Nouvelle contribution à la connaissance du genre *Xenylla* (Insecta: Collembola). *Khumbu Himal*, **4**, 152–5.
- Gama, M.M. da (1980). Aperçu évolutif d'une septantaine d'espèces et sous-espèces de *Xenylla* provenant de tous les continents. In *First International Seminar on Apterygota* (ed. R. Dallai), pp. 53–8. Accademia delle Scienze di Siena detta de'Fisiocritici, Siena.
- Gama, M.M. da (1984a). Phylogénie des espèces européennes de '*Pseudosinella*' (Collembola: Entomobryidae). *Annales de la Société Royale Zoologique de Belgique*, **114**, 59–70.
- Gama, M.M. da (1984b). Collemboles cavernicoles de l'Espagne. I. *Miscellània Zoològica (Barcelona)*, **8**, 81–7.
- Gama, M.M. da (1984c). Colêmbolos dos Açores II. *Boletim da Sociedade Portuguesa Entomologia*, **38**, 337–46.
- Gama, M.M. da (1985). Collemboles cavernicoles de l'Espagne. II. (Insecta, Apterygota). *Miscellània Zoològica (Barcelona)*, **9**, 209–14.
- Gama, M.M. da (1986a). Aperçu biogéographique des Collemboles de la Macaronesie. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 37–52. University of Siena, Siena.
- Gama, M.M. da (1986b). Systematique évolutive des *Xenylla*. XIV. Espèces provenant de Thaïlande, Bornéo, Australie et Norfolk, Galápagos, Mexique et Curaçao (Insecta: Collembola). *Revue Suisse de Zoologie*, **93**, 271–7.
- Gama, M.M. da (1987). Clef pour la détermination des espèces et sous-espèces de *Xenylla* à l'échelle mondiale (Insecta, Collembola). *Ciència Biológica (Ecol. Syst.)*, **7**, 45–55.
- Gama, M.M. da (1988a). Systematique évolutive des *Xenylla*. XV. Espèces provenant du Népal et de Sulawesi (Célèbes). *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **5**, (4), 53–61.
- Gama, M.M. da (1988b). Filogenia das espécies de *Xenylla* à escala mundial (Insecta, Collembola). *Evolucion Biológica*, **2**, 139–47.
- Gama, M.M. da (1988c). Colêmbolos das Canarias (Insectos, Apterigotas). *Actas III Congresso Ibérico de Entomologia, Granada*, 73–9.
- Gama, M.M. da (1988d). Systematique évolutive des *Pseudosinella*. XIV. Deux espèces nouvelles provenant des Açores (Insecta, Collembola). *Revue Suisse de Zoologie*, **95**, 607–11.
- Gama, M.M. da and Deharveng, L. (1984). *Haloxenylla*, nouveau genre halophile de Collembole Hypogastruridae. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **120**, 131–6.
- Gama, M.M. da and Greenslade, P. (1981). Relationships between the distribution and phylogeny of *Xenylla* (Collembola, Hypogastruridae) species in Australia and New Zealand. *Revue d'Écologie et de Biologie du Sol*, **18**, 269–84.
- Gama, M.M. da and Oliveira, E.P. de (1994). Evolutionary systematics of *Xenylla*. 16. Description of a new species in Amazonia (Insecta, Collembola). *Amazoniana*, **13**, 205–8.
- Gama, M.M. da, Múrias dos Santos, A.F.A., and Nogueira, A. (1989a). Comparaison de la composition de populations de Collemboles de peuplements d'Eucalyptus (*Eucalyptus globulus*) et de chene liege (*Quercus suber*). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 339–45. University of Siena, Siena.
- Gama, M.M. da, Lopes, C.M., and Nogueira, A. (1989b). Étude comparée de populations de Collemboles de plusieurs biotopes de l'Algarve (Portugal). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 363–70. University of Siena, Siena.
- Gama, M.M. da, Nogueira, A., Múrias dos Santos, A.F.A. (1991). Effects du reboisement par *Eucalyptus globulus* sur les Collemboles édaphiques. *Revue d'Écologie et de Biologie du Sol*, **28**, 9–18.

- Gama, M.M. da, Vasconcelos, T.M., and Sousa, J.P. (1994). Collembola diversity in Portuguese autochthonous and allochthonous forests. *Acta Zoologica Fennica*, **195**, 44–6.
- Gapud, V. (1971). Studies on Philippine Collembola. III. Suborder Arthropleona: Entomobryidae, with a checklist of Philippine Collembola. *Philippine Entomologist*, **2**, 1–50.
- Gasc, J.P., Betsch, J.M., and Massoud, Z. (1983). Prédation sélective des Collembolés par les Sauriens dans la litière de la forêt dense humide guyanaise. *Bulletin de la Société Zoologique de France*, **108**, 467–76.
- Geoffroy, E.L. (1762). *Histoire abrégée des insectes qui se trouvent aux environs de Paris*, 2. (Collembola on pp. 581–93, 605–14, 688–9).
- Geoffroy, E.L. (1799). *Histoire abrégée des insectes, dans laquelle ces animaux sont rangés suivant un ordre méthodique. Nouvelle édition, revue, corrigée et augmentée d'un Supplément considérable*. Calixte-Volland, Rémont, Paris.
- Gerdsmeyer, J. and Greven, H. (1987). Zur Kenntnis der Collembolenfauna des Eggegebirges. *Abhandlungen aus dem Westfälischen Museum für Naturkunde*, **49**, 1–49.
- Gerdsmeyer, J. and Greven, H. (1989). Der Einfluß von Säurestress auf die Energiegehalte von *Folsomia candida* (Collembola) und *Oniscus asellus* (Isopoda). *Verhandlungen der Gesellschaft für Ökologie*, **18**, 777–9.
- Gerdsmeyer, J. and Greven, H. (1991a). Collembolengemeinschaften eines Fichten- und eines Buchenwaldes im Sauerland. *Decheniana*, **144**, 129–40.
- Gerdsmeyer, J. and Greven, H. (1991b). Abundanz und Dominanz einiger Kleinarthropoden in Buchenwäldern des Eggegebirges, Nordrhein-Westfalen. *Acta Biologica Benrodis*, **3**, 1–26.
- Gerdsmeyer, J. and Greven, H. (1992). Synökologische und produktionsbiologische Untersuchungen an Collembolen aus Buchenwäldern des Eggegebirges (Westfalen). Ein Beitrag zur Immissionbelastung von Wäldern. *Abhandlungen aus dem Westfälischen Museum für Naturkunde*, **54**, 1–76.
- Gers, C. and Deharveng, L. (1985). Collembolés de l'Oukaimeden (Haut-Atlas de Marrakech, Maroc). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **121**, 51–61.
- Gers, C. and Najt, J. (1983). A note on Collembola (Insecta, Apterygota) found in a superficial underground compartment and a description of a new species of *Isotoma* (Desoria). *Revue d'Écologie et de Biologie du Sol*, **20**, 427–32.
- Gervais, P. (1844). Thysanoures. In Walkenaer's *Histoire naturelle des insectes aptères*, **3**, 377–456.
- Getzin, L.W. (1985). Chemical control of the springtail *Onychiurus pseudarmatus* (Collembola: Onychiuridae). *Journal of Economic Entomology*, **78**, 1337–40.
- Ghiradella, H. and Radigan, W. (1974). Collembolan cuticle: wax and antiwetting properties. *Journal of Insect Physiology*, **20**, 301–6.
- Gillott, C. (1995). *Entomology* (2nd edn). Plenum Press, New York.
- Gilmore, S.K. (1970). Collembola predation on nematodes. *Search-Agriculture*, **1**, (3), 1–12.
- Gilmore, S.K. and Potter, D.A. (1993). Potential role of Collembola as biotic mortality agents for entomopathogenic nematodes. *Pedobiologia*, **37**, 30–8.
- Gilmore, S.K. and Raffensperger, E.M. (1970). Foods ingested by *Tomocerus* spp. (Collembola: Entomobryidae), in relation to habitat. *Pedobiologia*, **10**, 135–40.
- Giribet, G., Carranza, S., Baguña, J., Riutort, M., and Ribera, C. (1996). First molecular evidence for the existence of a Tardigrada + Arthropoda clade. *Molecular Biology and Evolution*, **13**, 76–84.
- Gisin, H. (1943). Ökologie und Lebensgemeinschaften der Collembolen im schweizerischen Exkursionsgebiet Basels. *Revue Suisse de Zoologie*, **50**, 131–224.
- Gisin, H. (1944). *Hilfstabellen zum Bestimmen der holarktischen Collembolen*. Verlag Georg, Basel.
- Gisin, H. (1957). Sur la faune européenne des Collembolés I. *Revue Suisse de Zoologie*, **64**, 475–96.
- Gisin, H. (1958). Sur la faune européenne des Collembolés II. *Revue Suisse de Zoologie*, **65**, 773–8.
- Gisin, H. (1960a). *Collembolenfauna Europas*. Museum d'Histoire Naturelle, Genève.
- Gisin, H. (1960b). Collembolés cavernicoles de la Suisse, du Jura Français, de la Haute-Savoie et de la Bourgogne. *Revue Suisse de Zoologie*, **67**, 81–99.
- Gisin, H. (1960c). Sur la faune européenne des Collembolés III. *Revue Suisse de Zoologie*, **67**, 309–22.
- Gisin, H. (1961a). Collembolen aus der Sammlung C. Börner des deutschen Entomologischen Institutes (Apterygota). I. Deutschland und angrenzende Länder. *Beiträge zur Entomologie*, **11**, 329–54.
- Gisin, H. (1961b). Collembolen aus der Sammlung C. Börner des deutschen Entomologischen Institutes (Apterygota). II. Spitzbergen und Färöer. *Beiträge zur Entomologie*, **11**, 540–5.
- Gisin, H. (1962a). Collembolen aus österreichischen Höhlen (Insecta Apterygota). *Die Höhle, Wien*, **13**, 39–42.
- Gisin, H. (1962b). Typenuntersuchung, Variabilität und Gattungszugehörigkeit von *Hypogastrura cavicola* Börner. *Beiträge zur Entomologie*, **12**, 507–10.
- Gisin, H. (1962c). Sur la faune européenne des Collembolés IV. *Revue Suisse de Zoologie*, **69**, 1–23.
- Gisin, H. (1963a). Collembolés cavernicoles du Jura méridional et des chaînes subalpines. *Annales de Spéléologie*, **18**, 271–86.

- Gisin, H. (1963b). Collemboles d'Europe V. *Revue Suisse de Zoologie*, **70**, 77–101.
- Gisin, H. (1963c). Pour une réforme de la taxonomie appliquée aux Collemboles (Insectes Aptérygotes). *Archives des Sciences, Genève*, **16**, 211–16.
- Gisin, H. (1963d). Sieben neue Arten von Collembolen aus Bosnien und Wiederbeschreibung von *Onychiurus serratotuberculatus* Stach. *Godisnjak Bioloskog Instituta u Sarajevu*, **14**, 1–13.
- Gisin, H. (1964a). Collemboles d'Europe VI. *Revue Suisse de Zoologie*, **71**, 383–400.
- Gisin, H. (1964b). Collemboles d'Europe VII. *Revue Suisse de Zoologie*, **71**, 649–78.
- Gisin, H. (1964c). Apterygota. In *Fauna von Deutschland* (ed. P. Brohmer), pp. 143–9. Quelle and Meyer, Heidelberg.
- Gisin, H. (1967). La systématique idéale. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **5**, 111–28.
- Gisin, H. (1968). A cavity-slide technique for preparing permanent fluid preparations of small organisms. *Revue d'Écologie et de Biologie du Sol*, **4**, 581–3.
- Gisin, H. and Gama, M.M. da (1962). Les Siera des environs de Genève (Insecta, Collembola). *Revue Suisse de Zoologie*, **69**, 785–800.
- Glasgow, J.P. (1939). A population study of subterranean soil Collembola. *Journal of Animal Ecology*, **8**, 323–53.
- Gomez, M.A., Perez, M.T., and Sagardoy, M.A. (1990). Bacteries presentes dans le corps et les feces de *Proisotoma minuta* (Collembola: Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **27**, 449–57.
- Goto, H.E. (1955a). On the need for detailed descriptions of species of Collembola. *Entomologist's Monthly Magazine*, **91**, 238–9.
- Goto, H.E. (1955b). On some Malayan Collembola, including a description of *Salina pulchella*, sp.n. *Annals and Magazine of Natural History*, Series 12, **8**, 36–42.
- Goto, H.E. (1956). *Architomocerura* Denis, 1931 (Collemb., Isotomidae) an immature stage of *Tomocerus* Nicolet, 1841 (Collemb., Tomoceridae). *Entomologist's Monthly Magazine*, **92**, 49–51.
- Goto, H.E. (1960). Facultative parthenogenesis in Collembola. *Nature*, **188**, 958–9.
- Goto, H.E. (1961). Simple techniques for the rearing of Collembola and a note on the use of fungistatic substances in the cultures. *Entomologist's Monthly Magazine*, **96**, 138–40.
- Goto, H.E. (1964). On the use of chlorazol black as an aid to the identification of Collembola. *Pedobiologia*, **3**, 256–8.
- Goto, H.E. (1971). The effect of carbon dioxide anaesthesia on Collembola. *Michigan Entomologist*, **4**, 61–2.
- Goto, H.E. (1972a). On the structure and function of the mouthparts of the soil-inhabiting collembolan *Folsomia candida*. *Biological Journal of the Linnean Society*, **4**, 147–68.
- Goto, H.E. (1972b). Some observations on the biology and taxonomy of *Proisotoma stachi* Goto, 1957 (Insecta, Collembola: Isotomidae). *Journal of Natural History*, **6**, 195–202.
- Goto, H.E. and Delamare Deboutteville, C. (1953). *Anurida bisetosa* Bagnall, a synonym of *A. maritima* (Guérin) (Collemb., Hypogastruridae). *Entomologist's Monthly Magazine*, **89**, 249–50.
- Goto, H.E. and Delamare Deboutteville, C. (1954). *Anuridella hintoni* Bagnall, a synonym of *Anuridella marina* Willem (Collemb., Hypogastruridae). *Entomologist's Monthly Magazine*, **90**, 132–4.
- Goto, H.E. and Lawrence, P.N. (1960). A species of Collembola new to the British Isles. *Entomologist's Gazette*, **11**, 183.
- Goto, H.E. and Lawrence, P.N. (1964). On some new and disputed synonymy in British Collembola. *Proceedings of the Royal Entomological Society of London*, **33B**, 83–91.
- Goto, H.E. and Ögel, S. (1961). Variation in the mucro of *Folsomia candida* (Collembola: Isotomidae). *Entomologist*, May 1961, 105–7.
- Gough, H.J. (1973a). *Ptenothrix atra* (L.) (Collembola: Sminthuridae): possible confusion of immature specimens with *Dicyrtoma*. *Entomologist's Monthly Magazine*, **109**, 158.
- Gough, H.J. (1973b). The sensillae of the third antennal segment of the Symphypleona (Collembola). *Entomologist's Monthly Magazine*, **109**, 159–61.
- Gough, H.J. (1973c). *Sminthurides pseudassimilis* Stach, 1956, (Collembola: Sminthuridae). A re-examination of the structure of the antenna with new synonymy and designation of lectotypes. *Revue d'Écologie et de Biologie du Sol*, **12**, 649–54.
- Gough, H.J. (1977). A key for the identification of the families of Collembola recorded from the British Isles. *Entomologist's Monthly Magazine*, **113**, 193–7.
- Gough, H.J. (1978). The British insect fauna: check list – Collembola supplement. *Antenna*, **2**, 51.
- Gould, S.J. and Eldredge, N. (1993). Punctuated equilibrium comes of age. *Nature*, **366**, 223–7.
- Gouze, A. and Deharveng, L. (1987). Deux espèces nouvelles de *Pseudosinella* cavernicoles du Var (Coll.). *Bulletin de la Société Entomologique de France*, **91**, 65–8.
- Gray, J. and Shear, W. (1992). Early life on land. *American Scientist*, **80**, 444–56.

- Green, C.D. (1964). The life history and fecundity of *Folsomia candida* (Willem) var. *distincta* (Bagnall) (Collembola: Isotomidae). *Proceedings of the Royal Entomological Society of London*, **39A**, 125–8.
- Greenberg, Z. (1985). An unusual case of ectoparasitism by an insect of the Order Collembola. *Israel Journal of Medical Sciences*, **21**, 712.
- Greenslade, P. (1974). Ecological and geographical notes on Collembola of Kangaroo Island, South Australia. *Pedobiologia*, **14**, 256–65.
- Greenslade, P. (1977). A re-examination of the genus *Corynephoria* Absolon (Collembola: Sminthuridae). *Revue d'Écologie et de Biologie du Sol*, **14**, 241–56.
- Greenslade, P. (1981). Survival of Collembola in arid environments: observations in South Australia and the Sudan. *Journal of Arid Environments*, **4**, 219–28.
- Greenslade, P. (1982a). Origins of the collembolan fauna of arid Australia. In *Evolution of the flora and fauna of arid Australia* (ed. R. Barker and P.J.M. Greenslade), pp. 267–72. Peacock Publications, Adelaide.
- Greenslade, P. (1982b). Revision of the Spinothecinae (Collembola: Sminthuridae) including a new Australian genus. *Journal of the Australian Entomological Society*, **21**, 81–95.
- Greenslade, P. (1986a). Identity and synonymy of *Isotoma* (*Folsomotoma*) Bagnall (Isotomidae). In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 53–9. University of Siena, Siena.
- Greenslade, P. (1986b). Additions to the Collembolan fauna of Heard Island. *Records of the South Australian Museum*, **19**, 91–6.
- Greenslade, P. (1987). Generic biogeography of Tasmanian Collembola. In *Soil fauna and soil fertility* (ed. B.R. Striganova), pp. 653–60. Nauka, Moscow.
- Greenslade, P. (1988). Reply to R.A. Crowson's 'Comments on Insecta of the Rhynie Chert' (1985 *Entomol. Gener.* **11**, (1/2): 097–098). *Entomologia Generalis*, **13**, 115–17.
- Greenslade, P. (1989). Genera of Isotomidae with spined dentes from Southern regions. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 107–18. University of Siena, Siena.
- Greenslade, P. (1991a). Collembola (springtails). In *The Insects of Australia* Volume 1 (2nd edn) (ed. CSIRO), pp. 252–64. Carlton: Melbourne University Press.
- Greenslade, P. (1991b). Notes on Australian Uchidanurinae (Collembola: Neanuridae). In *Advances in management and conservation of soil fauna* (ed. G.K. Veeresh, D. Rajagopal, and C.A. Viraktamath), pp. 63–5. Oxford and IBH, New Delhi.
- Greenslade, P. (1992a). The identity of Australian specimens recorded as *Lepidosinella armata* Handschin 1920 (Collembola: Entomobryidae) with a key to Australian *Sinella* and *Coecobrya*. *Journal of the Australian Entomological Society*, **31**, 327–30.
- Greenslade, P. (1992b). New records of *Mesaphorura* (Collembola: Onychiuridae, Tullbergiinae) species from Australia, MacQuarie Island and the Antarctic. *Transactions of the Royal Society of South Australia*, **116**, 141–3.
- Greenslade, P. (1993). Australian native steppe-type landscapes: neglected areas for invertebrate conservation in Australia. In *Perspectives in insect conservation* (ed. K.J. Gaston, T.R. New, and M.J. Samways), pp. 51–73. Intercept, Andover, Hampshire.
- Greenslade, P. (1994a). Collembola. In *Zoological catalogue of Australia*, Volume 22. Protura, Collembola, Diplura (ed. W.W.K. Houston), pp. 19–138. CSIRO, Melbourne.
- Greenslade, P. (1994b). *Ptenothrix* (*Papirioides*) *tonsori* sp.n. (Collembola: Dicyrtomidae) from Sulawesi. *Acta Zoologica Fennica*, **195**, 47–51.
- Greenslade, P. (1995). Terrestrial invertebrates recorded in the territory. Appendix 4. In *Heard Island Wilderness Reserve Management Plan*, pp. 52–3. Australian Antarctic Division, Department of the Environment, Sport and Territories.
- Greenslade, P. and Crawford, I. (1994). A review of research on the invertebrates of western New South Wales. In *Future of the fauna of western New South Wales* (ed. D. Lunney, S. Hand, P. Reed, and D. Butcher), pp. 177–91. Royal Zoological Society of New South Wales, Australia.
- Greenslade, P. and Deharveng, L. (1984). *Caufrenyllodes* (Collembola: Odontellidae), a new genus from Australia. *Journal of the Australian Entomological Society*, **23**, 223–7.
- Greenslade, P. and Deharveng, L. (1986). *Psammisotoma*, a new genus of Isotomidae (Collembola) from marine littoral habitats. *Proceedings of the Royal Society of Queensland*, **97**, 89–95.
- Greenslade, P. and Deharveng, L. (1990). Australian species of the genus *Australonura* (Collembola: Neanuridae). *Invertebrate Taxonomy*, **3**, 565–93.
- Greenslade, P. and Deharveng, L. (1991). *Phradmon*, a new genus of Pleonurini (Collembola: Neanuridae) from Australia with a key to the genera from southern regions and notes on *Pronura*. *Invertebrate Taxonomy*, **5**, 837–54.

- Greenslade, P. and Fletcher, K.E. (1986). Collembola from earthworm rearing beds at Rothamsted, including three new records for Britain. *Entomologist's Monthly Magazine*, **122**, 143–4.
- Greenslade, P.J.M. and Greenslade, P. (1973). Epigaeic Collembola and their activity in a semi-arid locality in southern Australia during Summer. *Pedobiologia*, **13**, 227–35.
- Greenslade, P. and Greenslade, P.J.M. (1980). Relationships of some Isotomidae (Collembola) with habitat and other soil fauna. In *Soil biology as related to land use practices* (ed. D.L. Dindal), pp. 491–506. Environmental Protection Agency, Washington, D.C.
- Greenslade, P.J.M. and Greenslade, P. (1984). Soil surface insects of the Australian arid zone. In *Arid Australia* (ed. H.G. Cogger and E.E. Cameron), pp. 153–76. Australian Museum, Sydney.
- Greenslade, P. and Greenslade, P.J.M. (1987). Ecological strategies in Collembola: a new approach to the use of terrestrial invertebrates in environmental assessment. In *Soil fauna and soil fertility* (ed. B.R. Striganova), pp. 245–52. Nauka, Moscow.
- Greenslade, P.J.M. and Greenslade, P. (1989). Ground layer invertebrate fauna. In *Mediterranean landscapes in Australia – Mallee ecosystems and their management* (ed. J.C. Noble and R.A. Bradstock), pp. 266–84. CSIRO, Melbourne.
- Greenslade, P. and Ireson, J.E. (1986). Collembola of the southern Australian culture steppe and urban environments: a review of their pest status and key to identification. *Journal of the Australian Entomological Society*, **25**, 273–91.
- Greenslade, P. and Majer, J.D. (1980). Collembola of rehabilitated mine sites in western Australia. In *Soil biology as related to land use practices* (ed. D.L. Dindal), pp. 397–408. Environmental Protection Agency, Washington, D.C.
- Greenslade, P. and Majer, J.D. (1993). Recolonization by Collembola of rehabilitated bauxite mines in western Australia. *Australian Journal of Ecology*, **18**, 385–94.
- Greenslade, P. and Mott, J.J. (1982). Collembola and other soil and surface fauna of native and improved pastures at Katherine, Northern Territory. In *Proceedings of the 3rd Australian Conference on Grassland Invertebrate Ecology* (ed. K.E. Lee), pp. 299–307. CSIRO, Melbourne.
- Greenslade, P. and Najt, J. (1987a). Collembolles Brachystomellinae de l'Australie. I. Les genres *Brachystomella* et *Rapoportella*. *Annales de la Société Entomologique de France*, N.S., **23**, 435–53.
- Greenslade, P. and Najt, J. (1987b). Collembolles Brachystomellinae de l'Australie. II. Le genre *Salvarella* n.g. *Revue Française d'Entomologie*, N.S., **9**, 115–19.
- Greenslade, P. and Southcott, R.V. (1980). Parasitic mites on Sminthurid Collembola in Australia. *Entomologist's Monthly Magazine*, **116**, 85–7.
- Greenslade, P. and Sutrisno (1994). *Epimetrura rostrata* sp.n., *E. mirabilis* Schött, and the status of the genus *Epimetrura* (Collembola: Entomobryidae). *Acta Zoologica Fennica*, **195**, 52–7.
- Greenslade, P. and Thompson, C.H. (1981). Collembola from the Cooloola-Noosa River area, Queensland. *Proceedings of the Royal Society of Queensland*, **92**, 11–19.
- Greenslade, P. and Van Klinken, R.D. (1994). Marine littoral and coastal Collembola on the subantarctic Macquarie Island. *Acta Zoologica Fennica*, **195**, 58–61.
- Greenslade, P. and Whalley, P.E.S. (1986). The systematic position of *Rhyniella praecursor* Hirst and Maulik (Collembola), the earliest known hexapod. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 319–23. University of Siena, Siena.
- Greenslade, P. and Wise, K.A.J. (1984). Additions to the Collembolen fauna of the Antarctic. *Transactions of the Royal Society of South Australia*, **108**, 203–5.
- Greenslade, P. and Wise, K.A.J. (1986). Collembola of Macquarie Island. *Record of the Auckland Institute and Museum*, **23**, 67–97.
- Greenslade, P., Margules, C.R., and Adomeit, E.M. (1991). Distribution of Collembola in Eucalyptus forest in southeastern Australia. In *Advances in management and conservation of soil fauna* (ed. G.K. Veeresh, D. Rajagopal, and C.A. Viraktamath), pp. 53–62. Oxford and IBH, New Delhi.
- Grégoire-Wibo, C. (1974). Bioécologie de *Folsomia quadrioculata* (Insecta, Collembola). *Pedobiologia*, **14**, 199–207.
- Grégoire-Wibo, C. (1983). Incidences écologiques des traitements phytosanitaires en culture de betterave sucrière, essais expérimentaux en champ. I. Les Collembolles épigées. *Pedobiologia*, **25**, 37–48.
- Gressitt, J.L., Leech, R.E., and O'Brien, C.W. (1960). Trapping of air-borne insects in the Antarctic area I. *Pacific Insects*, **2**, 245–50.
- Greven, H., Gottwald, A., Rösgen, C., and Gerdsmeyer, J. (1991). Wie reagieren Collembolen auf Streusalz? Labor- und Freilanduntersuchungen. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **84**, 502–3.
- Grimnes, K.A. (1981). Esterases in *Folsomia candida* (Collembola: Isotomidae). Changes in isoenzyme titer during the moult cycle. *Pedobiologia*, **21**, 341–5.

- Grimnes, K.A. (1986). Esterases in *Folsomia candida* (Collembola: Isotomidae). Characterization of enzymes among parthenogenetic strains. *Comparative Biochemistry and Physiology*, **83C**, 359–63.
- Grinbergs, A. (1960). On mass occurrence and migration of Collembola. *Opuscula Entomologica*, **25**, 52–8.
- Grossmann, K. (1988). Zur rationellen Aufbereitung von Collembolen fangen. *Pedobiologia*, **32**, 363–6.
- Grow, A.B. and Christiansen, K. (1974). Chaetotaxy in nearctic *Friezea* (Collembola: Neanurinae) with notes on taxonomic use of chaetotaxy. *Revue d'Écologie et de Biologie du Sol*, **11**, 377–96.
- Grow, A. and Christiansen, K. (1976). Chaetotaxy in *Folsomia* (Collembola: Isotomidae) with special reference to nearctic species. *Revue d'Écologie et de Biologie du Sol*, **13**, 611–27.
- Gruia, M. (1983). Collemboles arthroploones de Cuba récoltes par les expéditions cubano-roumaines en 1969–1973, II. In *Resultats de expéditions cubano-roumaines à Cuba*, **4**, pp. 191–205. Acad. Rep. Sci., Bucharest.
- Gruia, M. (1984). Collemboles arthroploones de cuba récoltés par les expéditions cubano-roumaines en 1969–1973. *Travaux de l'Institut de Spéologie 'Emile Racovitza'*, **23**, 19–25.
- Gruttke, H., Kratz, W., Weigmann, G., and Haque, A. (1988). Terrestrial model food chain and environmental chemicals. I. Transfer of sodium [14C] pentachlorophenate between springtails and carabids. *Ecotoxicology and Environmental Safety*, **15**, 253–9.
- Guilbert, E., Baylac, E., and Najt, J. (1995). Canopy arthropod diversity in a New Caledonian primary forest sampled by fogging. *Pan Pacific Entomologist*, **71**, 3–12.
- Gullan, P.J. and Cranston, P.S. (1994). *The insects: an outline in entomology*. Chapman and Hall, London.
- Gunadi, B. (1994). Seasonal fluctuations of Collembola along the slope of a pine forest plantation in central Java. *Acta Zoologica Fennica*, **195**, 62–6.
- Gunn, A. and Cherrett, J.M. (1993). The exploitation of food resources by soil meso and macro invertebrates. *Pedobiologia*, **37**, 303–20.
- Guthrie, J.E. (1903). *The Collembola of Minnesota*. Reports of the Geological and Natural History Survey of Minnesota, Zoological Series, no. 4, pp. 1–110.
- Hågvar, S. (1982). Collembola in Norwegian coniferous forest soils. I. Relations to plant communities and soil fertility. *Pedobiologia*, **24**, 255–96.
- Hågvar, S. (1983). Collembola in Norwegian coniferous forest soils. II. Vertical distribution. *Pedobiologia*, **25**, 383–401.
- Hågvar, S. (1984). Effects of liming and artificial acid rain on Collembola and Protura in coniferous forest. *Pedobiologia*, **27**, 341–54.
- Hågvar, S. (1987a). Why do collemboles and mites react to changes in soil acidity? *Entomologiske Meddelelser*, **55**, 115–19.
- Hågvar, S. (1987b). Effects of artificial acid precipitation and liming on forest microarthropods. In *Soil fauna and soil fertility* (ed. B.R. Striganova), pp. 661–7. Nauka, Moscow.
- Hågvar, S. (1988). Decomposition studies in an easily-constructed microcosm: effects of microarthropods and varying soil pH. *Pedobiologia*, **31**, 293–303.
- Hågvar, S. (1990). Reactions to soil acidification in microarthropods: Is competition a key factor? *Biology and Fertility of Soils*, **9**, 178–81.
- Hågvar, S. (1994). Log-normal distribution of dominance as an indicator of stressed soil microarthropod communities. *Acta Zoologica Fennica*, **195**, 71–80.
- Hågvar, S. (1995). Long distance, directional migration on snow in a forest collembolan, *Hypogastrura socialis* (Uzel). *Acta Zoologica Fennica*, **196**, 200–5.
- Hågvar, S. and Abrahamsen, G. (1980). Colonisation by Enchytraeidae, Collembola and Acari in sterile soil samples with adjusted pH levels. *Oikos*, **34**, 245–58.
- Hågvar, S. and Abrahamsen, G. (1984). Collembola in Norwegian coniferous forest soils. III. Reactions to soil chemistry. *Pedobiologia*, **27**, 331–9.
- Hågvar, S. and Abrahamsen, G. (1990). Microarthropoda and Enchytraeidae (Oligochaeta) in a naturally lead-contaminated soil: a gradient study. *Environmental Entomology*, **19**, 1263–77.
- Hågvar, S. and Kjøndal, B.R. (1981a). Succession, diversity and feeding habits of microarthropods in decomposing birch leaves. *Pedobiologia*, **22**, 385–408.
- Hågvar, S. and Kjøndal, B.R. (1981b). Effects of artificial acid rain on the microarthropod fauna in decomposing birch leaves. *Pedobiologia*, **22**, 409–22.
- Hågvar, S., Østbye, E., and Melåen, J. (1978). Density of Collembola and Acarina in an alpine pioneer community near a glacier at Finse, South Norway. *Norwegian Journal of Entomology*, **25**, 229–30.
- Hale, W.G. (1963). The Collembola of eroding blanket bog. In *Soil organisms* (ed. J. Doeksen and J. Van der Drift), pp. 406–13. North Holland, Amsterdam.
- Hale, W.G. (1964a). A flotation method for extracting Collembola from agricultural soils. *Journal of Animal Ecology*, **33**, 363–9.

- Hale, W.G. (1964b). Experimental studies on the taxonomic status of some members of the *Onychiurus armatus* group. *Revue d'Écologie et de Biologie du Sol*, **1**, 501–10.
- Hale, W.G. (1965a). Observations on the breeding biology of Collembola. I. *Pedobiologia*, **5**, 146–52.
- Hale, W.G. (1965b). Observations on the breeding biology of Collembola. II. *Pedobiologia*, **5**, 161–77.
- Hale, W.G. (1965c). Post-embryonic development in some species of Collembola. *Pedobiologia*, **5**, 228–43.
- Hale, W.G. (1965d). The taxonomic status of some members of the *Onychiurus armatus* species group. *Proceedings of the 12th International Congress of Entomology*, London 1964. p. 111.
- Hale, W.G. (1966a). A population study of moorland Collembola. *Pedobiologia*, **6**, 65–99.
- Hale, W.G. (1966b). An experimental study of the taxonomic characters of *Lepidocyrtus lignorum* Fabricius 1775 sensu Gisin 1964. *Revue d'Écologie et de Biologie du Sol*, **3**, 293–300.
- Hale, W.G. (1968). A quantitative study of the morphological structures used as taxonomic criteria in the *Onychiurus armatus* group (Collembola, Onychiuridae). *Revue d'Écologie et de Biologie du Sol*, **3**, 493–514.
- Hale, W.G. (1969). Preliminary stereoscan studies of the genus *Onychiurus* Gervais (Collembola, Onychiuridae). In *The soil ecosystem*, Systematics Association Publication No. 8 (ed. J.G. Sheals), pp. 169–86. Systematics Association, London.
- Hale, W.G. (1980). Production and energy flow in two species of *Onychiurus* (Collembola, Insecta, Apterygota). *Pedobiologia*, **20**, 274–87.
- Hale, W.G. and Rowland, J.P.C. (1977). Biochemical 'fingerprints' as indicators of taxonomic status within the genus *Onychiurus*. *Revue d'Écologie et de Biologie du Sol*, **14**, 535–62.
- Hale, W.G. and Smith, A.L. (1966). Scanning electron microscope studies of cuticular structures in the genus *Onychiurus* (Collembola). *Revue d'Écologie et de Biologie du Sol*, **3**, 343–54.
- Hammer, M. (1953). Investigations on the microfauna of northern Canada. Part 2. Collembola. *Acta Antarctica*, **6**, 1–108.
- Hammond, P.M. (1994). Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society of London*, **345B**, 119–36.
- Handschin, E. (1921). Die Onychiuren der Schweiz. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, **32**, 1–37.
- Handschin, E. (1924). Neue myrmecophile und termitophile Collembolen formen aus Süd-Amerika. *Neue Beiträge zur Systematischen Insektenkunde*, **3**, (3), 13–19, 21–8.
- Handschin, E. (1929). Urinsekten oder Apterygota (Protura, Collembola, Diplura and Thysanura). *Die Tierwelt Deutschlands*, **16**, 1–150.
- Hanlon, R.D.G. (1981). Influence of grazing by Collembola on the activity of senescent fungal colonies grown on medium of different nutrient concentration. *Oikos*, **36**, 363–7.
- Hanlon, R.D.G. and Anderson, J.M. (1979). The effects of Collembola grazing on microbial activity in decomposing leaf litter. *Oecologia*, **38**, 93–9.
- Harper, J.L. and Hawksworth, D.L. (1994). Biodiversity: measurement and estimation. *Philosophical Transactions of the Royal Society of London*, **345B**, 5–12.
- Harris, K.K. and Boerner, R.E.J. (1990). Effects of below ground grazing by Collembola on growth, mycorrhizal infection, and P uptake of *Geranium robertianum*. *Plant and Soil*, **129**, 203–10.
- Harris, R.A. (1979). *A glossary of surface sculpturing*. Occasional Papers in Entomology, No. 28, State of California, Department of Food and Agriculture, Sacramento.
- Harrisson, P.M., Block, W., and Worland, M.R. (1990). Moisture and temperature dependent changes in the cuticular permeability of the Antarctic springtail *Parisotoma octoculata* (Willem). *Revue d'Écologie et de Biologie du Sol*, **27**, 435–48.
- Harrisson, P.M., Rothery, P., and Block, W. (1991). Drying processes in the Antarctic collembolan *Cryptopygus antarcticus* (Willem). *Journal of Insect Physiology*, **37**, 883–90.
- Hart, J.W. and Allamong, B.D. (1979). The role of esterase zymograms in collembolan species determination. *Revue d'Écologie et de Biologie du Sol*, **16**, 235–40.
- Hart, J.W. and Waltz, R.D. (1995). A new species and a new synonym in the *Hypogastrura* (s.str.) *nivicola* group (Collembola, Hypogastruridae). *Entomological News*, **106**, 77–80.
- Hasegawa, M. and Takeda, H. (1995). Changes in feeding attributes of four collembolan populations during the decomposition process of pine needles. *Pedobiologia*, **39**, 155–69.
- Hashimoto, H. and Tamura, H. (1994). Change in collembolan community during litter breakdown. *Acta Zoologica Fennica*, **195**, 67–8.
- Hassall, M., Visser, S., and Parkinson, D. (1986a). Vertical migration of *Onychiurus subtenis* (Collembola) in relation to rainfall and microbial activity. *Pedobiologia*, **29**, 175–82.
- Hassall, M., Parkinson, D., and Visser, S. (1986b). Effects of the collembolan *Onychiurus subtenis* on decomposition of *Populus tremuloides* leaf litter. *Pedobiologia*, **29**, 219–25.

- Haybach, G. (1992). Zur Collembolenfauna verschiedener Gebirgsstandorte in Österreich. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Österreich*, **129**, 159–214.
- Hazelton, M. (1972). Vice county records of fauna collected from the hypogean and related zones. *Transactions of the Cave Research Group of Great Britain*, **14**, 232–73.
- Hazelton, M. (1974a). Irish Vice county records of fauna collected from the hypogean and related zones. *Transactions of the Cave Research Group of Great Britain*, **15**, 203–15.
- Hazelton, M. (1974b). A checklist of the Irish cave fauna. Trogloxene, troglophile and troglobite. *Transactions of the Cave Research Group of Great Britain*, **15**, 221–2.
- Hazelton, M. (1974c). Hypogean fauna recorded from Ireland 1952–1971. *Transactions of the Cave Research Group of Great Britain*, **15**, 225–52.
- Healey, I.N. (1967). An ecological study of temperatures in a Welsh moorland soil. 1962–1963. *Journal of Animal Ecology*, **36**, 425–34.
- Hedlund, K., Ek, H., Gunnarsson, T., and Svegborn, C. (1990). Male choice and male competition in *Orchesella cincta* (Collembola). *Experientia*, **46**, 524–6.
- Hedlund, K., Bengtsson, G., and Rundgren, S. (1995). Fungal odour discrimination in two sympatric species of fungivorous collembolans. *Functional Ecology*, **9**, 869–75.
- Hedlund, K., Boddy, L., and Preston, C.M. (1991). Mycelial responses of the soil fungus, *Mortierella isabellina*, to grazing by *Onychiurus armatus* (Collembola). *Soil Biology and Biochemistry*, **23**, 361–6.
- Heisler, C. (1991). Einfluss von Gefuegeschaden infolge mechanischer Belastung auf die Springschwanz – Besiedelung einer konventionell bewirtschafteten Ackerfläche (Collembola). *Entomologia Generalis*, **16**, 39–52.
- Heisler, C. (1994). Auswirkungen von Bodenverdichtungen auf die Bodenmesofauna: Collembola und Gamasina – ein dreijähriger Feldversuch. *Pedobiologia*, **38**, 566–76.
- Heisler, C. and Kaiser, E.A. (1995). Influence of agricultural traffic and crop management on Collembola and microbial biomass in arable soil. *Biology and Fertility of Soils*, **19**, 159–65.
- Hemmer, W. (1990). Karyotype differentiation and chromosomal variability in springtails (Collembola, Insecta). *Biology and Fertility of Soils*, **9**, 119–25.
- Hermosilla, W., Keuck, G., and Rubio, I. (1984a). Essai d'application de la taxonomie numérique à 23 espèces de Collemboles néarctiques du genre *Folsomia* Willem, 1902 (Insecte Collembola Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **21**, 87–100.
- Hermosilla, W., Thibaud, J.M., and Keuck, G. (1984b). Essai d'application de la taxonomie numérique au genre *Schaefferia* Absolon, 1900 (Insecte Collembola Poduromorphe). *Revue d'Écologie et de Biologie du Sol*, **21**, 101–4.
- Hermosilla, W., Thibaud, J.M., and Keuck, G. (1985). Essai d'application de la taxonomie numérique au genre *Bonetogastrura* Thibaud 1974 et *Typhlogastrura* Bonet, 1930 (Insecte Collembola Poduromorphe). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **7**, 637–57.
- Hertzberg, K., Leinaas, H.P., and Ims, R.A. (1994). Patterns of abundance and demography: Collembola in a habitat patch gradient. *Ecography*, **17**, 349–59.
- Heungens, A. and Van Daele, E. (1984). The influence of some acids, bases and salts on the mite and Collembola population of a pine litter substrate. *Pedobiologia*, **27**, 299–311.
- Heywood, V.H. (ed.) (1995). *Global biodiversity assessment*. Cambridge University Press.
- Higgins, R.C. (1982). Predation of *Notiophilus* (Coleoptera, Carabidae) on Collembola as a predator-prey teaching model. *Journal of Biological Education*, **16**, 128–30.
- Hijii, N. (1987). Seasonal changes in abundance and spatial distribution of the soil arthropods in a Japanese Cedar (*Cryptomeria japonica* D. Don) plantation, with special reference to Collembola and Acarina. *Ecological Research*, **2**, 159–73.
- Hijii, N. (1989). Arthropod communities in a Japanese Cedar (*Cryptomeria japonica* D. Don) plantation: abundance, biomass and some properties. *Ecological Research*, **4**, 243–60.
- Hijii, N. (1994). Abundance patterns of soil micro-arthropods at a *Pinus pumila* scrub in an alpine range of central Japan. *Ecological Research*, **9**, 175–83.
- Hill, J. (1752). *A general natural history: or, new and accurate descriptions of the animals, vegetables and minerals of the different parts of the world*. Vol.I, Fossils; Vol. II, Plants; Vol. III, Animals. Thomas Osborne, London.
- Hingley, M.R. (1971). The ascomycete fungus *Daldinia concentrica* as a habitat for animals. *Journal of Animal Ecology*, **40**, 17–32.
- Hintzpeter, U. and Bauer, T. (1986). The antennal trap of the ground beetle *Loricera pilicornis*: a specialization for feeding on Collembola. *Journal of Zoology*, **208**, 615–30.
- Hiol, F.H., Dixon, R.K., and Curl, E.A. (1994). The feeding preference of mycophagous Collembola varies with the ectomycorrhizal symbiont. *Mycorrhiza*, **5**, 99–103.

- Hippa, H., Koponen, S., Mannila, R., and Vilkamaa, P. (1988). Invertebrates of Scandinavian caves. VI. Collembola. *Notulae Entomologicae*, **68**, 1–5.
- Hisamatsu, M. and Matsunaga, M. (1994). Life cycle of the collembolans *Tomocerus cuspidatus* Börner and *Entomobrya aino* Matsumura and Ishida. *Acta Zoologica Fennica*, **195**, 69–70.
- Hisamatsu, M., Itoh, R., and Takahashi, T. (1986). Life cycle of a collembolan species *Entomobrya aino* (Matsumura et Ishida). *Daigaku Kyoyubu Kiyo*, **17**, 63–70.
- Hodkinson, I.D., Healey, V., and Coulson, S. (1994a). Moisture relationships of the high arctic collembolan *Onychiurus arcticus*. *Physiological Entomology*, **19**, 109–14.
- Hodkinson, I.D., Coulson, S., Webb, N.R., Block, W., Strathdee, A.T., and Bale, J.S. (1994b). Feeding studies on *Onychiurus arcticus* (Tullberg) (Collembola, Onychiuridae) on West Spitsbergen. *Polar Biology*, **14**, 17–20.
- Hoekstra, J.A. and Van Ewijk, P.H. (1993). Alternatives for the no-observed-effect level. *Environmental Toxicology and Chemistry*, **12**, 187–94.
- Hogervorst, R.F., Verhoef, H.A., and Van Straalen, N.M. (1993). Five-year trends in soil arthropod densities in pine forests with various levels of vitality. *Biology and Fertility of Soils*, **15**, 189–95.
- Holdaway, F.G. (1927). The bionomics of *Sminthurus viridis* or the South Australian lucerne flea. *Commonwealth of Australia Council for Scientific and Industrial Research, Melbourne*, Pamphlet No. 4, 1–23.
- Hölldobler, B. and Wilson, E.O. (1990). *The ants*. Springer Verlag, Berlin, Heidelberg.
- Honma, K. (1988). Food habit of the garden springtail *Bourletiella hortensis* Fitch, in relation to its importance as a sugar beet pest (Collembola: Sminthuridae). *Japanese Journal of Applied Entomology and Zoology*, **32**, 305–9.
- Hook, R. (1665). *Micrographia; or some physiological descriptions of minute bodies made by magnifying glasses with observations and inquiries there upon*. Royal Society, London.
- Hopkin, S.P. (1989). *Ecophysiology of metals in terrestrial invertebrates*. Elsevier Applied Science, Barking.
- Hopkin, S.P. (1990). Critical concentrations, pathways of detoxification and cellular ecotoxicology of metals in terrestrial arthropods. *Functional Ecology*, **4**, 321–7.
- Hopkin, S.P. (1993a). Ecological implications of '95% protection levels' for metals in soils. *Oikos*, **66**, 137–41.
- Hopkin, S.P. (1993b). In situ biological monitoring of pollution in terrestrial and aquatic ecosystems. In *Handbook of ecotoxicology* Volume 1 (ed. P. Calow), pp. 397–427. Blackwell, Oxford.
- Hopkin, S.P. (1994). Effects of metal pollutants on decomposition processes in terrestrial ecosystems with special reference to fungivorous soil arthropods. In *Toxic metals in soil-plant systems* (ed. S.M. Ross), pp. 303–26. John Wiley, Chichester.
- Hopkin, S.P. (1995). Deficiency and excess of essential and non-essential metals in terrestrial insects. *Symposia of the Royal Entomological Society of London*, **17**, 251–70.
- Hopkin, S.P. (in press). Ecotoxicology, biodiversity and the species concept with special reference to springtails (Collembola). In *Ecological principles for risk assessment of contaminants in soil* (ed. N.M. Van Straalen and H. Løkke), Chapman and Hall, London.
- Hopkin, S.P. and Read, H.J. (1992). *Biology of millipedes*. Oxford University Press.
- Hopkin, S.P., Watson, K., Martin, M.H., and Mould, M.L. (1985). The assimilation of heavy metals by *Lithobius variegatus* and *Glomeris marginata* (Chilopoda: Diplopoda). *Bijdragen tot de Dierkunde*, **55**, 88–94.
- Hopkin, S.P., Hames, C.A.C., and Dray, A. (1989). X-ray microanalytical mapping of the intracellular distribution of pollutant metals. *Microscopy and Analysis*, **14**, 23–7.
- Hove, K., Pedersen, Ø., Garmo, T.H., Hansen, H.S., and Staaland, H. (1990). Fungi: a major source of radiocesium contamination of grazing ruminants in Norway. *Health Physics*, **59**, 189–92.
- Hrivnak, L. (1983). Synusies of Collembola in nests of small mammals of the High Tatras and hypsomertic distribution of individual collembolan species. *Biologia*, **38**, 555–67.
- Huhta, V. and Mikkonen, M. (1982). Population structure of Entomobryidae (Collembola) in a mature spruce stand and in clear-cut reforested areas in Finland. *Pedobiologia*, **24**, 231–40.
- Huhta, V., Hyvönen, R., Kaasalainen, P., Koskenniemi, A., Muona, J., Mäkelä, I., Sulander, M., and Vilkamaa, P. (1986). Soil fauna of Finnish coniferous forests. *Acta Zoologica Fennica*, **23**, 345–60.
- Humbert, W. (1974a). Localisation, structure et genèse des concrétions minérales dans le mésentéron des Collembolles Tomoceridae (Insecta, Collembola). *Zeitschrift für Morphologie der Tiere*, **78**, 93–109.
- Humbert, W. (1974b). Étude du pH intestinal d'un Collembole (Insecta, Apterygote). *Revue d'Écologie et de Biologie du Sol*, **11**, 89–97.

- Humbert, W. (1975). Ultrastructure des nephrocytes cephaliques et abdominaux chez *Tomocerus minor* (Lubbock) et *Lepidocyrtus curvicolis* Bourlet (Collemboles). *International Journal of Insect Morphology and Embryology*, **4**, 307–18.
- Humbert, W. (1977). The mineral concentrations in the midgut of *Tomocerus minor* (Collembola): microprobe analysis and physiological significance. *Revue d'Écologie et de Biologie du Sol*, **14**, 71–80.
- Humbert, W. (1978a). Intracellular and intramitochondrial binding of lanthanum in dark degenerating midgut cells of a Collembolan (Insect). *Histochemistry*, **59**, 117–28.
- Humbert, W. (1978b). Cytochemistry and X-ray microprobe analysis of the midgut of *Tomocerus minor* Lubbock (Insecta, Collembola) with special reference to the physiological significance of the mineral concretions. *Cell and Tissue Research*, **187**, 397–416.
- Humbert, W. (1979a). *Les organes excréteurs des Collemboles: étude ultrastructurale, cytochimique, spectrographique et approche écophysologique*. PhD thesis, University of Strasbourg.
- Humbert, W. (1979b). The midgut of *Tomocerus minor* Lubbock (Insecta, Collembola): ultrastructure, cytochemistry, ageing and renewal during a moult cycle. *Cell and Tissue Research*, **196**, 39–57.
- Humbert, W. (1980). Intracellular accumulation of uranium and lead in collembolan (insect). In *38th Annual proceedings of the Electron Microscopical Society of America* (ed. G.W. Bailey), pp. 564–5. Electron Microscopical Society of America, San Francisco.
- Humbert, W. (1981). Excretion et detoxication de quelques métaux lourds chez les collemboles (insectes). *Bulletin de l'Association Philomathique d'Alsace et de Lorraine*, **18**, 97–101.
- Humbert, W. and Barra, J.A. (1979). Les Collemboles: un modele d'étude de l'absorption intestinale de l'excretion et de la detoxication de quelques métaux lourds. *Bulletin de la Société Ecophysologie*, **4**, 117–21.
- Hunter, B.A., Johnson, M.S., and Thompson, D.J. (1987). Ecotoxicology of copper and cadmium in a contaminated grassland ecosystem. II. Invertebrates. *Journal of Applied Ecology*, **24**, 587–99.
- Hurd, P.D. (1954). 'Myiasis' resulting from the use of the aspirator method in the collection of insects. *Science*, **119**, 814–15.
- Hurej, M. and Pomorski, R.J. (1989). Collembola of sugar beet fields in Lower Silesia. *Polskie Pismo Entomologiczne*, **59**, 367–75.
- Hurej, M., Debek, J., and Pomorski, R.J. (1992). Investigations on damage to sugar beet seedlings by the springtail *Onychiurus armatus* (Collembola, Onychiuridae) in Lower Silesia (Poland). *Acta Entomologica Bohemoslovaca*, **89**, 403–7.
- Hutasse, F. (1982). Renouvellement cyclique de l'épithélium du mésentéron chez deux Collemboles entomobryomorphes (Insectes, Aptérygotes). *Annales des Sciences Naturelles, Zoologie*, **4**, 41–61.
- Hutasse-Jennenot, F. (1974). A film on biology of *Sphaeridia pumilis* (Symphyleona, Collembola, Insecta). *Pedobiologia*, **14**, 177.
- Hüther, W. (1962). Beitrag zur Gattung *Willemia* Börner. *Beiträge zur Entomologie*, **12**, 511–26.
- Hüther, W. (1970). Über einige Collembolen von den Kanarischen Inseln. *Commentationes Biologicae*, **31**, 1–11.
- Hüther, W. (1986). New aspects in taxonomy of *Lepidocyrtus* (Collembola). In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 61–5. University of Siena, Siena.
- Hutson, B.R. (1978a). Effects of the variations of the plaster-charcoal culture method on a collembolan *Folsomia candida*. *Pedobiologia*, **18**, 138–44.
- Hutson, B.R. (1978b). Influence of pH, temperature and salinity on the fecundity and longevity of four species of Collembola. *Pedobiologia*, **18**, 163–79.
- Hutson, B.R. (1980a). Colonization of industrial reclamation sites by Acari, Collembola and other invertebrates. *Journal of Applied Ecology*, **17**, 255–75.
- Hutson, B.R. (1980b). The influence of soil development on the invertebrate fauna colonizing industrial reclamation sites. *Journal of Applied Ecology*, **17**, 277–86.
- Hutson, B.R. (1981). Age distribution and the annual reproductive cycle of some Collembola colonizing reclaimed land in Northumberland, England. *Pedobiologia*, **21**, 410–16.
- Hutson, B.R. and Veitch, L.G. (1983). Mean annual population density of Collembola and Acari in the soil and litter of three indigenous South Australian forests. *Australian Journal of Ecology*, **8**, 113–26.
- Hutson, B.R. and Veitch, L.G. (1987). Densities of Collembola and Acarina in the soil and litter of three indigenous South Australian forests related to layer, site and seasonal differences. *Australian Journal of Ecology*, **12**, 239–61.
- Hwang, U.W., Lee, B.H., and Kim, W. (1995). Sequences of the 18S rDNAs from two collembolan insects: shorter sequences in the V4 and V7 regions. *Gene*, **154**, 293–4.
- Imms, A.D. (1906). *Anurida*. Liverpool Marine Biology Committee, Memoirs on Typical British Marine Plants and Animals, No. 13. Williams and Norgate, London.
- Imms, A.D. (1925). *A general textbook of entomology*. Methuen, London.

- Ineson, P., Leonard, M.A., and Anderson, J.M. (1982). Effect of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter. *Soil Biology and Biochemistry*, **14**, 601–5.
- Ireson, J.E. (1982). A re-examination of the distribution of the pasture snout mite, *Bdellodes lapidaria* (Kramer) (Acari: Bdellidae) and the lucerne flea, *Sminthurus viridis* (L.) (Collembola: Sminthuridae) in Tasmania. *Journal of the Australian Entomological Society*, **21**, 251–5.
- Ireson, J.E. (1984). The effectiveness of *Bdellodes lapidaria* (Kramer) (Acari: Bdellidae) as a predator of *Sminthurus viridis* (L.) (Collembola: Sminthuridae) in North West Tasmania. *Journal of the Australian Entomological Society*, **23**, 185–91.
- Ireson, J.E. (1993). Activity and pest status of surface-active Collembola in Tasmanian field crops and pastures. *Journal of the Australian Entomological Society*, **32**, 155–67.
- Ireson, J.E. and Greenslade, P. (1990). *Lasofinus* gen.n. (Collembola: Tomoceridae) from Tasmania and a re-examination of *Neophoriella dubia* Womersley (Tomoceridae). *Journal of the Australian Entomological Society*, **29**, 205–14.
- Ireson, J.E. and Paterson, S.C. (1991). Progress on the biological control of Lucerne flea (*Sminthurus viridis* (L.)) with the Spiny Snout mite (*Neomolgus capillatus* (Kramer)) in Tasmania. In *Proceedings of the National Workshop on the redlegged earth mite*, pp. 98–103. Perth, Australia
- Itoh, R. (1985). A new species of the genus *Sminthurus* (Collembola: Sminthuridae) from the Japanese red pines at Fujiyoshida, Central Japan. *Daigaku Kyoyubu Kiyo*, **16**, 83–7.
- Itoh, R. (1991). Growth and life cycle of an arboreal Collembola, *Xenylla brevispina* Kinoshita, with special reference to its seasonal migration between tree and forest floor. *Edaphologia*, **45**, 33–48.
- Itoh, R. (1994a). Life cycle of the collembolan *Sminthurus arborealis* Itoh, a species active in winter on trees. *Acta Zoologica Fennica*, **195**, 87–8.
- Itoh, R. (1994b). A new species of the genus *Lipothrix* (Collembola, Sminthuridae) from Japan. *Edaphologia*, **51**, 13–17.
- Itoh, R. and Zhao, L.J. (1993a). Two new species of Symphypleona (Collembola) from the Tian-mu mountains in East China. *Edaphologia*, **50**, 31–6.
- Itoh, R. and Zhao, L.J. (1993b). A new species of the genus *Papirioides* (Collembola, Sminthuridae) from Xishuangbanna, China. *Japanese Journal of Entomology*, **61**, 847–51.
- Itoh, R., Hisamatsu, M., Matsunaga, M., and Takahashi, T. (1985). Preliminary study on the life cycle of a collembolan species, *Papirinus prodigiosus* Yosii, making use of an extremely large Tullgren funnel. *Daigaku Kyoyubu Kiyo*, **16**, 75–81.
- Jablonska, A., Szklarzewicz, T., Larink, O., and Bilinski, S. (1993). Structure of ovaries in two collembolans, *Allacma fusca* and *Arrhopalites coecus* (Hexapoda, Entognatha). *Folia Histochemica et Cytobiologica*, **31**, 87–92.
- Jaeger, G. and Eisenbeis, G. (1984). pH-dependent absorption of solutions by the ventral tube of *Tomocerus flavescens* (Tullberg, 1871) (Insecta, Collembola). *Revue d'Écologie et de Biologie du Sol*, **21**, 519–31.
- Jamieson, B.G.M. (1987). *The ultrastructure and phylogeny of insect spermatozoa*. Cambridge University Press.
- Janetschek, H. (1967). Growth and maturity of the springtail *Gomphiocephalus hodgsoni* Carpenter, from South Victoria Land and Ross Island. *Antarctic Research Series*, **10**, 295–305.
- Janssen, G.M. and Joosse, E.N.G. (1987). Reproduction and growth in Collembola under laboratory conditions. *Pedobiologia*, **30**, 1–8.
- Janssen, G.M., De Jong, G., Joosse, E.N.G., and Scharloo, W. (1988). A negative maternal effect in springtails. *Evolution*, **42**, 828–34.
- Janssen, M.P.M. and Bedaux, J.J.M. (1989). Importance of body-size for cadmium accumulation by forest litter arthropods. *Netherlands Journal of Zoology*, **39**, 194–207.
- Janssen, M.P.M. and Bergema, W.F. (1991). The effect of temperature on cadmium kinetics and oxygen consumption in soil arthropods. *Environmental Toxicology and Chemistry*, **10**, 1493–1501.
- Janssen, M.P.M. and Hogervorst, R.F. (1993). Metal accumulation in soil arthropods in relation to micro-nutrients. *Environmental Pollution*, **79**, 181–9.
- Janssen, M.P.M., Joosse, E.N.G., and Van Straalen, N.M. (1990). Seasonal variation in concentration of cadmium in litter arthropods from a metal contaminated site. *Pedobiologia*, **34**, 257–67.
- Janssen, M.P.M., Bruins, A., De Vries, T.H., and Van Straalen, N.M. (1991). Comparison of cadmium kinetics in four soil arthropod species. *Archives of Environmental Contamination and Toxicology*, **20**, 305–12.
- Janssen, M.P.M., Ma, W.C., and Van Straalen, N.M. (1993). Biomagnification of metals in terrestrial ecosystems. *Science of the Total Environment*, Supplement 1993, 511–24.
- Jeffrey, C. (1989). *Biological nomenclature*. Edward Arnold, London.
- Johnson, D.L. and Wellington, W.G. (1980a). Post-embryonic growth of the collembolans *Folsomia candida* and *Xenylla grisea* at three temperatures. *Canadian Entomologist*, **112**, 687–95.

- Johnson, D.L. and Wellington, W.G. (1980b). Predation of *Apochthonius minimus* (Pseudoscorpionida, Chthonidae) on *Folsomia candida* (Collembola, Isotomidae). 1. Predation rate and size-selection. *Researches on Population Ecology*, **22**, 339–52.
- Johnson, D.L. and Wellington, W.G. (1980c). Predation of *Apochthonius minimus* (Pseudoscorpionida, Chthonidae) on *Folsomia candida* (Collembola, Isotomidae). 2. Effects of predation on prey populations. *Researches on Population Ecology*, **22**, 353–65.
- Johnson, D.L. and Wellington, W.G. (1983). Dispersal of the collembolan *Folsomia candida* Willem, as a function of age. *Canadian Journal of Zoology*, **61**, 2534–8.
- Jonston, J. (1657). *A history of the wonderful things of nature. Set forth on ten severall classes. Rendred into English by a person of quality (John Rowland)*. J. Streater, London.
- Jonstonus, J. (1657). *Historiae naturalis de insectis libri III*. Apud Joannem Jacobi Fil. Schipper, Amsterdam.
- Joosse, E.N.G. (1965). Pitfall-trapping as a method for studying surface dwelling Collembola. *Zeitschrift für Morphologie und Ökologie der Tiere*, **55**, 587–96.
- Joosse, E.N.G. (1966). Some observations on the biology of *Anurida maritima* (Guérin) (Collembola). *Zeitschrift für Morphologie und Ökologie der Tiere*, **57**, 320–8.
- Joosse, E.N.G. (1969). Population structure of some surface dwelling Collembola in a coniferous forest soil. *Netherlands Journal of Zoology*, **19**, 621–34.
- Joosse, E.N.G. (1970). The formation and biological significance of aggregations in the distribution of Collembola. *Netherlands Journal of Zoology*, **20**, 299–314.
- Joosse, E.N.G. (1971). Ecological aspects of aggregation in Collembola. *Revue d'Écologie et de Biologie du Sol*, **8**, 91–7.
- Joosse, E.N.G. (1976). Littoral apterygotes (Collembola and Thysanura). In *Marine insects* (ed. L. Cheng), pp. 151–86. North Holland, Amsterdam.
- Joosse, E.N.G. (1981). Ecological strategies and population regulation of Collembola in heterogeneous environments. *Pedobiologia*, **21**, 346–56.
- Joosse, E.N.G. (1983). New developments in the ecology of Apterygota. *Pedobiologia*, **25**, 217–34.
- Joosse, E.N.G. and Buker, J.B. (1979). Uptake and excretion of lead by litter-dwelling Collembola. *Environmental Pollution*, **18**, 235–40.
- Joosse, E.N.G. and Groen, J.B. (1970). Relationships between saturation deficit and the survival and locomotory activity of surface dwelling Collembola. *Entomologia Experimentalis et Applicata*, **13**, 229–35.
- Joosse, E.N.G. and Kapteijn, J.M. (1968). Activity-stimulating phenomena caused by field-disturbance in the use of pitfall traps. *Oecologia*, **1**, 385–92.
- Joosse, E.N.G. and Koelman, T.A.C.M. (1979). Evidence for the presence of aggregation pheromones in *Onychiurus armatus* (Collembola), a pest insect in sugar beet. *Entomologia Experimentalis et Applicata*, **26**, 197–201.
- Joosse, E.N.G. and Testerink, G.J. (1977). The role of food in the population dynamics of *Orchesella cincta* (Linné) (Collembola). *Oecologia*, **29**, 189–204.
- Joosse, E.N.G. and Veltkamp, E. (1970). Some aspects of growth, moulting and reproduction in five species of surface dwelling Collembola. *Netherlands Journal of Zoology*, **20**, 315–28.
- Joosse, E.N.G. and Verhoef, H.A. (1974). On the aggregational habits of surface dwelling Collembola. *Pedobiologia*, **14**, 245–9.
- Joosse, E.N.G. and Verhoef, S.C. (1983). Lead tolerance in Collembola. *Pedobiologia*, **25**, 11–18.
- Joosse, E.N.G. and Verhoef, H.A. (1987). Developments in ecophysiological research on soil invertebrates. *Advances in Ecological Research*, **16**, 175–248.
- Joosse, E.N.G., Brugman, F.A., and Veld, C.J. (1973). The effects of constant and fluctuating temperatures on the production of spermatophores and eggs in populations of *Orchesella cincta* (Linné), (Collembola, Entomobryidae). *Netherlands Journal of Zoology*, **23**, 488–502.
- Jordana, R. (1980). Estudio faunístico del Macizo de Quinto Real (Pirineos Occidentales). IV. Genero *Hypogastrura* (Collembola, Hypogastruridae). *Publicaciones de Biología de la Universidad de Navarra*, **5**, 1–30.
- Jordana, R. (1993). Two new Poduromorpha from Navarra (Spain) (Insecta, Collembola). *Spixiana*, **16**, 19–24.
- Jordana, R. and Arbea, J.I. (1989a). Descripción de una nueva especie de *Seira* Lubbock, 1869 (Collembola, Entomobryidae) procedente de Navarra (España). *Eos*, **65**, 87–91.
- Jordana, R. and Arbea, J.I. (1989b). Redescription of *Pseudachorudina angelieri* Cassagnau, 1959 (Collembola: Pseudachorutinae). *Graellsia*, **45**, 75–7.
- Jordana, R. and Arbea, J.I. (1989c). Clave de identificación de los géneros de Colémbolos de España (Insecta: Collembola). *Publicaciones de Biología de la Universidad de Navarra*, **19**, 1–16.
- Jordana, R. and Arbea, J.I. (1990a). Una nueva especie de Collembola (Isotomidae) de Navarra (N. de la Península Ibérica). *Redia*, **73**, 423–35.

- Jordana, R. and Arbea, J.I. (1990b). Especies Ibericas de *Hypogastrura* (*Ceratophysella*) de seis ojos con descripcion de tres nuevas especies (Collembola, Hypogastruridae). *Graellsia*, **46**, 161–73.
- Jordana, R. and Arbea, J.I. (1990c). *Hypogastrura* (s.str.) *conflictiva* sp.n. (Collembola, Hypogastruridae) de la Peninsula Ibérica. *Miscellània Zoològica (Barcelona)*, **14**, 59–63.
- Jordana, R. and Arbea, J.I. (1992). *Xenyllogastrura steineri* n.sp. y su comparacion con las especies del mismo genero, presentes en la Peninsula Iberica Islas Canarias (Collembola, Hypogastruridae). *Boletín de la Asociacion Española de Entomologia*, **16**, 11–17.
- Jordana, R. and Arbea, J.I. (1994). Contribucion al conocimiento de las especies de *Mesaphorura* europeas y descripcion de dos especies nuevas para la Peninsula Ibérica. *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **24**, 1–13.
- Jordana, R. and Asiain, A. (1981). Estudio de *Friesea* en Navarra con decripcion de una nueva forma dentro del grupo *Friesea subterranea*. *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **6**, 47–59.
- Jordana, R. and Beruete, E. (1983). Cavernicolous Collembola from karst caves in the west of Navarra (Spain). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **56**, 303–15.
- Jordana, R., Arbea, J.I., Moraza, L., Montenegro, E., Mateo, M.D., Hernandez, M.A., and Herrera, L. (1987). Effect of reafforestation by conifers in natural biotopes of middle and south Navarra (Northern Spain). *Revue Suisse de Zoologie*, **94**, 491–502.
- Jordana, R., Arbea, J.I., and Arino, A.H. (1990). Catálogo de Colémbolos Ibéricos. Base de datos. *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **21**, 1–231.
- Jørgensen, S.E., Nielsen, S.N., and Jørgensen, L.A. (1991) (eds.). *Handbook of ecological parameters and ecotoxicology*. Elsevier Science, Amsterdam.
- Joy, V.C. and Chakravorty, P.P. (1991). Impact of pesticides on nontarget microarthropod fauna in agricultural soil. *Ecotoxicology and Environmental Safety*, **22**, 8–16.
- Juberthie, C. and Cassagnau, P. (1971). L'évolution du système neurosécréteur chez les Insectes; l'importance des Collembolés et des autres Aptérygotes. *Revue d'Écologie et de Biologie du Sol*, **8**, 59–80.
- Juberthie, C. and Decu, V. (1994) (eds.). *Encyclopaedia biospeologica*. Société de Biospéologie (CNRS), Moulis: Academie Roumaine Bucarest.
- Juberthie, C. and Massoud, Z. (1977). Étude ultrastructurale des poils sécréteurs de cire chez *Dicyrtoma atra* L. (Collembola, Dicyrtomidae). *Revue d'Écologie et de Biologie du Sol*, **14**, 125–37.
- Jura, C. (1965). Embryonic development of *Tetradontophora bielensis* (Waga) (Collembola) from oviposition until germ band formation stage. *Acta Biologica Cracoviensia, Zoologie*, **8**, 141–57.
- Jura, C. (1966). Origin of the endoderm and embryogenesis of the alimentary system in *Tetradontophora bielensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **9**, 93–102.
- Jura, C. (1967a). Origin of germ cells and gonads formation in embryogenesis of *Tetradontophora bielensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **10**, 97–103.
- Jura, C. (1967b). The signification and function of the primary dorsal organ in embryonic development of *Tetradontophora bielensis* (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **10**, 301–11.
- Jura, C. (1972). Development of Apterygote insects. In *Development systems: insects*, Volume 1, pp. 49–94. Academic Press, London.
- Jura, C. and Krzystofowicz, A. (1977). Ultrastructural changes in embryonic midgut cells developing into larval midgut epithelium of *Tetradontophora bielensis* (Waga) Collembola. *Revue d'Écologie et de Biologie du Sol*, **14**, 103–15.
- Jura, C. and Krzystofowicz, A. (1982). Scanning electron microscopy of *Tetradontophora bielensis* (Waga) (Collembola) embryogenesis – fertilized egg to 64 blastomere stage. *Acta Biologica Academiae Scientiarum Hungaricae*, **33**, 39–48.
- Jura, C. and Krzystofowicz, A. (1986). Scanning electron microscopy of *Tetradontophora bielensis* (Waga) (Collembola) embryogenesis: segmentation and appendage formation of head. *Acta Biologica Cracoviensia, Zoologie*, **28**, 7.
- Jura, C. and Krzystofowicz, A. (1992). Initiation of embryonic development in *Tetradontophora bielensis* (Waga) (Collembola: Onychiuridae) eggs: meiosis, polyspermy, union of gametes and first cleavage. *International Journal of Insect Morphology and Embryology*, **21**, 87–94.
- Kaiser, P.A. and Lussenhop, J. (1991). Collembolan effects on establishment of vesicular-arbuscular mycorrhizae in soybean (*Glycine max*). *Soil Biology and Biochemistry*, **23**, 307–8.
- Kamplichler, C. (1990). Community structure and vertical distribution of Collembola and Cryptostigmata in a dry-turf cushion plant. *Biology and Fertility of Soils*, **9**, 130–4.
- Kamplichler, C. (1992). Community structure and phenology patterns of epedaphic Collembola in a dry-turf grassland. *Zoologische Jahrbücher für Systematik*, **119**, 369–81.
- Kamplichler, C. and Hauser, M. (1993). Roughness of soil pore surface and its effect on available habitat space of microarthropods. *Geoderma*, **56**, 223–32.

- Kaprus, I.J. and Szeptycki, A. (1992). A new species of the genus *Drepanura* (Collembola, Entomobryidae) from south Siberia. *Zoologicheskyy Zhurnal*, **71**, 143–6.
- Kaprus, I.J. and Weiner, W.M. (1994). Two interesting species of Onychiurinae (Collembola) from Ukraine and some remarks on *Allaphorura franzi* (Stach, 1946). *Acta Zoologica Cracoviensia*, **37**, 59–64.
- Karuhize, G.R. (1971). The structure of the postantennal organ in *Onychiurus* sp. (Insecta: Collembola) and its connections to the central nervous system. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **118**, 263–82.
- Kato, M. (1995). The aspidistra and the amphipod. *Nature*, **377**, 293.
- Keilbach, R. (1982). Bibliographie und Liste der Arten tierischer Einschlüsse in fossilen Harzen sowie ihrer Aufbewahrungsorte. *Deutsche Entomologische Zeitschrift*, **29**, 129–286, 301–491.
- Kellert, S.R. (1993). Values and perceptions of invertebrates. *Conservation Biology*, **7**, 845–55.
- Kennedy, A.D. (1994). Simulated climate change: a field manipulation study of polar microarthropod community response to global warming. *Ecography*, **17**, 131–40.
- Kevan, P.G. and Kevan, D.K. McE. (1970). Collembola as pollen feeders and flower visitors with observations from the high Arctic. *Quaestiones Entomologicae*, **6**, 311–26.
- Khanislamova, G.M. (1986). New species of springtails of the genus *Onychiurus* (Collembola, Onychiuridae) from the CIS-Ural region. *Zoologicheskyy Zhurnal*, **65**, 1470–8.
- Kiauta, B. (1970). Review of the germ cell chromosome cytology of Collembola with a list of chromosome numbers and data on two species new to cytology. *Gen. e. Phaen.*, **4**, 89–99.
- Kilbertus, G. and Vannier, G. (1981). Relations microflore-microfauna dans la grotte de Saint Catherine (Pyrénées Ariégeoises). II. Le regime alimentaire de *Tomocerus minor* (Lubbock) et *Tomocerus problematicus* Cassagnau (Insectes Collembolés). *Revue d'Écologie et de Biologie du Sol*, **18**, 319–38.
- King, K.L. and Hutchinson, K.J. (1980). The effects of superphosphate and stocking intensity on grassland microarthropods. *Journal of Applied Ecology*, **17**, 581–91.
- King, K.L., Hutchinson, K.J., and Greenslade, P. (1976). The effects of sheep numbers on associations of Collembola in sown pastures. *Journal of Applied Ecology*, **13**, 731–9.
- King, K.L., Greenslade, P., and Hutchinson, K.J. (1985). Collembolan associations in natural versus improved pastures of the New England Tableland, NSW: Distribution of native and introduced species. *Australian Journal of Ecology*, **10**, 421–7.
- King, P.E., Pugh, P.J.A., Fordy, M.R., Love, N., and Wheeler, S.A. (1990). A comparison of some environmental adaptations of the littoral collembolans *Anuridella marina* (Willem) and *Anurida maritima* (Guérin). *Journal of Natural History*, **24**, 673–88.
- Kisiel, E., Kubrakiewicz, J., and Bilinski, S.M. (1994). Formation of the egg envelope in the collembolan, *Orchesella flavescens* (Entognatha, Collembola). *Zoologica Poloniae*, **39**, 69–78.
- Kiss, I. and Bakonyi, G. (1990). Pesticide tests with Collembola. *Agrokémia és Talajtan*, **39**, 586–8.
- Klag, J. (1982a). Germ line of *Tetrodontophora bielanensis* (Insecta, Collembola). Ultrastructural study on the origin of primordial germ cells. *Journal of Embryology and Experimental Morphology*, **72**, 183–95.
- Klag, J. (1982b). Germ line of *Tetrodontophora bielanensis* (Insecta, Collembola). 2. Ultrastructural differentiation of primordial germ cells during early embryogenesis. *Cytobios*, **33**, 173–82.
- Klag, J. (1983a). Germ line of *Tetrodontophora bielanensis* (Insecta, Collembola). 3. Migration of primordial germ cells. *Cytobios*, **38**, 51–63.
- Klag, J. (1983b). Germ line of *Tetrodontophora bielanensis* (Insecta, Collembola). Comparative analysis of primordial germ cells formation and differentiation in embryogenesis of insects. *Postepy Biologii Komorki*, **10**, 289–316.
- Klag, J. (1984). Germ line of *Tetrodontophora bielanensis* (Insecta, Collembola). 4. Nucleolus-like bodies extruded *in toto* from the nuclei of primordial germ cells become part of the 'nuage'. *Cytobios*, **40**, 7–20.
- Klag, J. and Ksiazkiewicz-Kapralaska, M. (1989). Embryonic hemocytes and body cavity formation in *Tetrodontophora bielanensis* (Insecta, Collembola). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 215–19. University of Siena, Siena.
- Klag, J. and Ksiazkiewicz-Kapralaska, M. (1990). Embryonic hemocytes and body cavity formation in *Tetrodontophora bielanensis* (Insecta, Collembola). *Cytobios*, **64**, 175–80.
- Klag, J. and Witalis, J. (1990). Differentiation of somatic cells in the embryonic gonad of *Tetrodontophora bielanensis* (Waga) (Collembola). *Zoologischer Anzeiger*, **224**, 236–44.
- Klag, J., Ksiazkiewicz, M., and Rosciszewska, E. (1981). The ultrastructure of the midgut in *Xenylla grisea* (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **23**, 47–52.
- Klauer, E. (1975). Some aspects of the reproductive biology of *Bourletiella* (*Cassagnaudiella*) *pruinosa* (Tullberg, 1871) (Collembola: Sminthuridae). *Bulletin Zoologisch Museum, Universiteit van Amsterdam*, **4**, (20), 179–86.

- Kleuters, K. and Greven, H. (1992). Veränderungen des Transportepithels im Ventraltubus von *Folsomia candida* (Collembola) nach Belastung mit den Streusalzen NaCl und CMA nebst Anmerkungen zur Struktur dieses Organs. *Acta Biologica Benrodis*, **4**, 87–116.
- Klironomos, J.N. and Kendrick, B. (1995a). Relationships among microarthropods, fungi, and their environment. *Plant and Soil*, **170**, 183–97.
- Klironomos, J.N. and Kendrick, B. (1995b). Stimulative effects of arthropods on endomycorrhizas of sugar maple in the presence of decaying litter. *Functional Ecology*, **9**, 528–36.
- Klironomos, J.N., Widden, P., and Deslandes, I. (1992). Feeding preferences of the collembolan *Folsomia candida* in relation to microfungal successions on decaying litter. *Soil Biology and Biochemistry*, **24**, 685–92.
- Kloet, G.S. and Hincks, W.D. (1964). *A check list of British insects. Part I. Small orders and Hemiptera*. 2nd edn. Royal Entomological Society, London.
- Knight, C.B. (1963). The microstratification of *Tomocerus* (Collembola) in a beech-maple forest of North Carolina. *American Midland Naturalist*, **70**, 187–96.
- Knight, C.B. and Angel, R.A. (1967). A preliminary study of the dietary requirements of *Tomocerus* (Collembola). *American Midland Naturalist*, **77**, 510–17.
- Knight, C.B. and Chesson, J.P. (1966). The effect of DDT on the forest floor Collembola of a loblolly pine stand. *Revue d'Écologie et de Biologie du Sol*, **3**, 129–39.
- Knight, C.B. and Read, V. (1969). Microstratification of *Tomocerus* (Collembola) in a pine-open field continuum. *Revue d'Écologie et de Biologie du Sol*, **6**, 221–34.
- Kniss, V.A. (1985). Springtails of the genus *Schaefferia* (Collembola, Hypogastruridae) from caves of Southwest Bashkiria. *Zoologicheskoy Zhurnal*, **64**, 934–7.
- Kniss, V. and Thibaud, J.M. (1995). Une nouvelle espèce de *Philotella* des grottes d'Oural du Sud (Collembola, Neanuridae, Pseudachorutinae). *Revue Française d'Entomologie*, N.S., **17**, 49–51.
- Kojima, K. (1985). The life history of *Hypogastrura denisana* in culture situation (Collembola: Hypogastruridae). *Edaphologia*, **32**, 1–10.
- Koledin, D., Ribarac-Stepic, N., and Stankovic, J. (1981). Participation of *Tetradontophora bielensis* (Collembola, Insecta) in decomposition of forest litter lipid compounds. *Pedobiologia*, **22**, 71–6.
- Koo, Y.H. and Deharveng, L. (1990). A note on the springtail fauna (Class Collembola) of Ulu Kinchin, Pahang, Malaysia. *Malayan Nature Journal*, **43**, 274–5.
- Kopeszki, H. (1988). Zur biologie zweier hochalpiner Collembolen – *Isotomurus palliceps* (Uzel, 1891) und *Isotoma saltans* (Nicolet, 1841). *Zoologische Jahrbücher für Systematik*, **115**, 405–39.
- Kopeszki, H. (1991). Abundanz und Abbauleistung der Mesofauna (Collembolen) als Kriterien für die Bodenzustandsdiagnose im Wiener Buchenwald. *Zoologischer Anzeiger*, **227**, 136–59.
- Kopeszki, H. (1992a). Veränderungen der Mesofauna eines Buchenwaldes bei Säurebelastung. *Pedobiologia*, **36**, 295–305.
- Kopeszki, H. (1992b). Versuch einer aktiven Bioindikation mit den bodenlebenden Collembolen-Arten *Folsomia candida* (Willem) und *Heteromurus nitidus* (Templeton) in einem Buchenwald-Ökosystem. *Zoologischer Anzeiger*, **228**, 82–90.
- Kopeszki, H. (1993a). Auswirkungen von Düngergaben auf die Mesofauna, insbesondere Collembolenfauna, verschiedener Waldstandorte im Böhmerwald. *Zoologischer Anzeiger*, **231**, 83–98.
- Kopeszki, H. (1993b). Auswirkungen von Säure- und Stickstoff-Deposition auf die Mesofauna, insbesondere Collembolen. *Forstw. Cbl.*, **112**, 88–92.
- Kopeszki, H. (1994). Revitalisierungsdüngung von Fichtenbeständen: Einfluss auf Bodentiere. *Forstliche Schriftenreihe Universität für Bodenkultur Wien*, **7**, 99–108.
- Kopeszki, H. and Jandl, R. (1994). Die Mesofauna, insbesondere Collembolenfauna, im Buchen Wienerwald in Abhängigkeit von Streu-Akkumulation und Depletion. *Zoologischer Anzeiger*, **233**, 123–34.
- Kopeszki, H. and Meyer, E. (1994). Artenzusammensetzung und Abundanz von Collembolen in Waldböden Voralbergs (Österreich). *Bericht des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck*, **81**, 151–66.
- Kopeszki, H. and Trockner, V. (1994). Auswirkungen des Skibetriebs auf die Collembolenfauna einer alpinen Wiese im Grödenal (South Tyrol). *Zoologischer Anzeiger*, **233**, 221–39.
- Korr, H. (1968). Das postembryonale Wachstum verschiedener Hirnbereiche bei *Orchesella villosa* L. (Ins. Collembola). *Zeitschrift für Morphologie der Tiere*, **62**, 389–422.
- Kováč, L. (1994). Effects of soil type on collembolan communities in agroecosystems. *Acta Zoologica Fennica*, **195**, 89–93.
- Kowal, N.E. and Crossley, D.A. (1971). The ingestion rates of microarthropods in pine mor estimated with radioactive calcium. *Ecology*, **52**, 444–52.
- Kozlov, D.P. (1986). Collembola as possible intermediate hosts of *Avitellina arctica* (Cestoda, Anoplocephalata). *Parazitologiya*, **20**, 73–4.

- Krishnan, G. (1969). Chemical components and mode of hardening of the cuticle of Collembola. *Acta Histochemica*, **34**, 212–28.
- Kristensen, N.P. (1991). Phylogeny of extant hexapods. In *The Insects of Australia* Volume 1 (2nd edn) (ed. CSIRO), pp. 125–40. Carlton: Melbourne University Press.
- Krogh, P.H. (1991). Perturbation of the soil microarthropod community with the pesticides benomyl and isophenos. I. Population changes. *Pedobiologia*, **35**, 71–88.
- Krogh, P.H. (1994). *Microarthropods as bioindicators: a study of disturbed populations*. PhD thesis, National Environmental Research Institute, Silkeborg, Denmark.
- Krogh, P.H. (1995a). Does a heterogeneous distribution of food or pesticide affect the outcome of toxicity tests with Collembola? *Ecotoxicology and Environmental Safety*, **30**, 158–63.
- Krogh, P.H. (1995b). Effects of pesticides on the reproduction of *Hypoaspis aculeifer* (Gamasida: Laelapidae) in the laboratory. *Acta Zoologica Fennica*, **196**, 333–7.
- Kronshage, J. (1992). Experimente zur Wirkung von Bleiverbindungen und Sauern auf Collembolen (Insecta, Collembola). *Zoologische Beiträge*, **34**, 289–311.
- Krool, S. and Bauer, T. (1987). Reproduction, development and pheromone secretion in *Heteromurus nitidus* Templeton, 1835 (Collembola, Entomobryidae). *Revue d'Écologie et de Biologie du Sol*, **24**, 187–95.
- Krzysztofowicz, A. (1967a). Spermatogenesis in *Tetrodontophora bielanensis* (Waga) (Collembola). *Zeszyty Naukowe Uniwersytetu Jagiellońskiego, Prace Zoologiczne*, **164**, 27–70.
- Krzysztofowicz, A. (1967b). Postembryonic development of male reproductive system in *Tetrodontophora bielanensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **10**, 289–99.
- Krzysztofowicz, A. (1971). Histochemical and autoradiographic analysis of RNA synthesis in trophic cells of the female gonad of *Tetrodontophora bielanensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **14**, 299–305.
- Krzysztofowicz, A. (1977). Les études comparatives sur la morphologie des ovaires chez les Collembolles. *Revue d'Écologie et de Biologie du Sol*, **14**, 81–90.
- Krzysztofowicz, A. (1980a). Ultrastructure of the spermatophores in *Tetrodontophora bielanensis* (Waga) (Collembola). *Folia Biologica Krakow*, **28**, 77–82.
- Krzysztofowicz, A. (1980b). The ultrastructure of spermatogonia and germ cells of the germarium in *Tetrodontophora bielanensis* (Waga) (Collembola, Apterygota). *Folia Biologica Krakow*, **28**, 363.
- Krzysztofowicz, A. (1986a). Ultrastructural studies on embryonic development of *Tetrodontophora bielanensis* (Waga) (Collembola): formation of the first and second blastodermal cuticles. 1. TEM studies. *Acta Biologica Cracoviensia, Zoologie*, **28**, 19.
- Krzysztofowicz, A. (1986b). Ultrastructural studies of embryonic development of *Tetrodontophora bielanensis* (Waga) (Collembola) – formation of the first and second blastodermal cuticles. 2. SEM studies. *Acta Biologica Cracoviensia, Zoologie*, **28**, 27.
- Krzysztofowicz, A. and Antoniklema, J. (1981). The occurrence of paracrystalline inclusions in oocytes and trophocytes of the ovary of *Tetrodontophora bielanensis* (Waga) (Collembola). *Folia Biologica Krakow*, **29**, 3.
- Krzysztofowicz, A. and Byczkowska-Smyk, W. (1966). Preliminary investigations on the fine structure of spermatozoa of *Tetrodontophora bielanensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **9**, 251–8.
- Krzysztofowicz, A. and Kisiel, E. (1986). Morphogenesis of first egg envelope in *Tetrodontophora bielanensis* (Waga) (Collembola). Preliminary studies. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 281–5. University of Siena, Siena.
- Krzysztofowicz, A. and Kisiel, E. (1989). Further studies on the morphogenesis and second egg envelopes of *Tetrodontophora bielanensis* (Waga) (Collembola). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 221–8. University of Siena, Siena.
- Krzysztofowicz, A., Klag, J., and Komorowska, B. (1972). The fine structure of the cuticle in *Tetrodontophora bielanensis* (Waga) Collembola. *Acta Biologica Cracoviensia, Zoologie*, **85**, 113–19.
- Krzysztofowicz, A., Jura, C., Jura, C., and Bilinski, S. (1973). Ultrastructure of midgut epithelial cells of *Tetrodontophora bielanensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **16**, 257–65.
- Kseneman, M. (1936). Schlüssel zur Bestimmung aller bisher bekannten Arten der Gattung *Folsomia* Willem 1902. *Sbornik Československé Akademie Zemedelských Ved, Prague*, **11**, 210–19.
- Ksiazkiewicz-Ilijewa, M. and Rosciszewska, E. (1979). Ultrastructure of the hemocytes of *Tetrodontophora bielanensis* Waga (Collembola). *Cytobios*, **26**, 113–21.
- Kubiena, W.L. (1953). *The soils of Europe*. Thomas Murby, London.
- Kukalová-Peck, J. (1987). New Carboniferous Diplura, Montura, and Thysanura, the hexapod ground plan, and the role of thoracic side lobes in the origin of wings (Insecta). *Canadian Journal of Zoology*, **65**, 2327–45.

- Kukalová-Peck, J. (1991). Fossil history and the evolution of hexapod structures. In *The Insects of Australia* Volume 1 (2nd edn) (ed. CSIRO), pp. 141–79. Carlton: Melbourne University Press.
- Kukalová-Peck, J. (1992). The 'Uniramia' do not exist: The ground plan of the Pterygota as revealed by Permian Diaphanopteroidea from Russia (Insecta: Paleodictyopteroidea). *Canadian Journal of Zoology*, **70**, 236–55.
- Kula, E. (1992). *The effects of pollutants on arthropods (a bibliography)*. Faculty of Forestry, Brno, Czechoslovakia.
- Kuznetsova, N.A. and Potapov, M.B. (1988). New data on the taxonomy of springtails of the Family Neanuridae and Odontellidae (Collembola). *Zoologicheskyy Zhurnal*, **67**, 1833–44.
- Lagerlöf, J. and Andrén, O. (1985). Succession and activity of microarthropods and enchytraeids during barley straw decomposition. *Pedobiologia*, **28**, 343–57.
- Lagerlöf, J. and Andrén, O. (1991). Abundance and activity of Collembola, Protura and Diplura (Insecta, Apterygota) in four cropping systems. *Pedobiologia*, **35**, 337–50.
- Lamarck, J.B. (1801). *Système des animaux sans vertèbres ou tables général des classes, des ordres et des genres des animaux*. L'auteur et Deterville, Paris.
- Lambert, M.R.K. (1973). A vertical succession of Collembola and their relationship to other arthropods in Irish woodland. *Entomologist's Monthly Magazine*, **108**, 240–7.
- Larink, O. and Bilinski, S. (1989). Fine structure of the egg envelopes of one proturan and two collembolan genera (Apterygota). *International Journal of Insect Morphology and Embryology*, **18**, 39–45.
- Lartey, R.T., Curl, E.A., and Peterson, C.M. (1986). Compared biological control of *Rhizoctonia solani* by fungal agents and mycophagous Collembola. *Phytopathology*, **76**, 1104.
- Lartey, R.T., Curl, E.A., and Peterson, C.M. (1988). Effects of *Trichoderma harzianum* and *Gliocladium virens* on mycophagous Collembola (Insecta), *Proisotoma minuta* and *Onychiurus encarpatus*. *Phytopathology*, **78**, 628.
- Lartey, R.T., Curl, E.A., Peterson, C.M., and Harper, J.D. (1989). Mycophagous grazing and food preference of *Proisotoma minuta* (Collembola: Isotomidae) and *Onychiurus encarpatus* (Collembola: Onychiuridae). *Environmental Entomology*, **18**, 334–7.
- Lartey, R.T., Curl, E.A., Peterson, C.M., and Williams, J.C. (1991). Control of *Rhizoctonia solani* and cotton seedling disease by *Laetisaria arvalis* and a mycophagous insect *Proisotoma minuta* (Collembola). *Journal of Phytopathology*, **133**, 89–98.
- Lartey, R.T., Curl, E.A., and Peterson, C.M. (1994). Interactions of mycophagous Collembola and biological control fungi in the suppression of *Rhizoctonia solani*. *Soil Biology and Biochemistry*, **26**, 81–88.
- Lasebikan, B.A. (1971). The relationship between temperature and humidity and the efficient extraction of Collembola by a dynamic-type method. *Revue d'Écologie et de Biologie du Sol*, **8**, 287–93.
- Lasebikan, B.A., Betsch, J.M., and Dallai, R. (1980). A new genus of Symphyleona (Collembola) from West Africa. *Systematic Entomology*, **5**, 179–83.
- Laskowski, R. (1991). Are the top carnivores endangered by heavy metal biomagnification? *Oikos*, **60**, 387–90.
- Laskowski, R. (1995). Some good reasons to ban the use of NOEC, LOEC and related concepts in ecotoxicology. *Oikos*, **73**, 140–4.
- Latreille, P.A. (1806). *Genera crustaceorum et insectorum*. Amand Koenig, Paris.
- Latreille, P.A. (1810). *Considération générales sur l'ordre naturel des animaux composant des classes des Crustacés des Arachnides et des insectes avec un tableau methodiques de leurs genres disposés en familles*. Deterville, Paris.
- Lauga-Reyrel, F. (1977). Contribution à l'étude du cycle biologique saisonnier de *Neanura monticola* (Collembola): aspects histologiques. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **113**, 83–124.
- Lauga-Reyrel, F. (1979). Étude histologique du cycle saisonnier d'*Hypogastrura tullbergi* (Collembola) et des conséquences de l'écomorphose. *Archives de Zoologie Expérimentale et Générale*, **120**, 195–218.
- Lauga-Reyrel, F. (1980). Aspect histophysiologique de l'écomorphose. I. Étude ultrastructurale du mesenteron chez *Hypogastrura tullbergi* (Collembola). *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **2**, 1–11.
- Lauga-Reyrel, F. (1981). Aspect histophysiologique de l'écomorphose. II. Étude ultrastructurale du corps gras chez *Hypogastrura tullbergi* (Collembola). *Annales des Sciences Naturelles, Zoologies et Biologies Animales*, **3**, 115–28.
- Lauga-Reyrel, F. (1984a). Étude anatomique et ultrastructurale des organes neurohémaux et des corps allatés d'*Hypogastrura tullbergi* (Tullberg) (Collembola: Hypogastruridae). *International Journal of Insect Morphology and Embryology*, **13**, 399–410.

- Lauga-Reyrel, F. (1984b). Modifications ultrastructurales des corps allates au cours du développement et de l'ecomorphose chez *Hypogastrura tullbergi* (Tullberg) (Collembola; Hypogastruridae). *International Journal of Insect Morphology and Embryology*, **13**, 411–24.
- Lauga-Reyrel, F. (1984c). Aspect histophysiologique de l'ecomorphose. III. Étude ultrastructurale des modifications cuticulaires d'*Hypogastrura tullbergi* (Collembola). *Annales des Sciences Naturelles, Zoologies et Biologies Animale*, **6**, 71–100.
- Lauga-Reyrel, F. (1984d). Aspect histophysiologique de l'ecomorphose. IV. Étude ultrastructurale des hémocytes et leur évolution en relation avec celle du corps gras pendant l'ecomorphose chez *Hypogastrura tullbergi* (Collembola). *Annales des Sciences Naturelles, Zoologies et Biologies Animale*, **6**, 177–90.
- Lauga-Reyrel, F. (1986). Presence des cavités intracellulaires énigmatiques dans l'épiderme des Collembolles Neanuridae. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 295–99. University of Siena, Siena.
- Lavell, P., Blanchart, E., Martin, A., Martin, A., Spain, A., Toutain, F., Barois, I., and Schaefer, R. (1993). A hierarchical model for decomposition in terrestrial ecosystems – application to soils of the humid tropics – special review paper. *Biotropica*, **25**, 130–50.
- Lawrence, P.N. (1959). Cavernicolous Collembola collections. *Transactions of the Cave Research Group of Great Britain*, **52**, 117–31.
- Lawrence, P.N. (1961a). Variation in *Hypogastrura* (H.) *viatica* (Tullberg, 1872) (Collembola). *Entomologist*, **94**, 151–4.
- Lawrence, P.N. (1961b). A survey of the Collembola of the Burren, Co. Clare, Ireland. *Entomologist's Gazette*, **12**, 143–64.
- Lawrence, P.N. (1962). A review of Bagnall's *Hypogastrura* types (Collembola). *Entomologist's Gazette*, **13**, 132–51.
- Lawrence, P.N. (1963a). Collembola from Buckingham Palace gardens. *Proceedings of the South London Entomological and Natural History Society*, Part II, 1963, 76–7.
- Lawrence, P.N. (1963b). A review of Bagnall's *Friesia* types (Collembola). *Entomologist*, **96**, 20–2.
- Lawrence, P.N. (1966). A redescription of *Sminthurus viridis* (Collembola, Insecta) with notes on related species. *Revue d'Écologie et de Biologie du Sol*, **3**, 511–21.
- Lawrence, P.N. (1968). Synonyms of *Uzelia setifera* Absolon, 1901 (Collembola: Isotomidae). *Entomologist's Gazette*, **19**, 59–64.
- Lawrence, P.N. (1969a). Isotomidae from the Solomon Islands (Collembola). *Pacific Insects*, **11**, 545–59.
- Lawrence, P.N. (1969b). Soil fauna studies illustrated by Collembola. Part I. Taxonomy and geographical distribution of the Collembola. *Philosophical Transactions of the Royal Society of London*, **255B**, 307–12.
- Lawrence, P.N. (1970a). Collembola (springtails) of sewage filters. *Waste and Water Treatment*, **13**, 106–9.
- Lawrence, P.N. (1970b). La faune terrestre de l'Île de Sainte-Hélène. I. Collembola. *Annales du Musée Royal de l'Afrique Centrale, Zoologiques*, **181**, 135–46.
- Lawrence, P.N. (1973a). Collembola. In *Monks Wood. A nature reserve record* (ed. R.C. Steele and R.C. Welch), pp. 125–8. Nature Conservancy, Natural Environment Research Council, Abbots Ripton.
- Lawrence, P.N. (1973b). The species of *Folsomia* Willem, 1902 (Collembola) described by Bagnall. *Entomologist's Gazette*, **24**, 349–61.
- Lawrence, P.N. (1975). The formation of ornamentation in collembolan cuticle. *Revue d'Écologie et de Biologie du Sol*, **12**, 473–5.
- Lawrence, P.N. (1977). Studies on the tibiotarsal chaetotaxy of Collembola. *Systematic Entomology*, **2**, 313–17.
- Lawrence, P.N. (1978a). The terminology of terminalia and cartography of chaetotaxy in the Collembola, its evolutionary significance and systematic utility. In *First International Seminar on Apterygota* (ed. R. Dallai), pp. 69–80. Accademia delle Scienze di Siena detta de' Fisiocritici, Siena.
- Lawrence, P.N. (1978b). *Cryptopygus sverdrupi* n.sp. A new species of Collembola (Isotomidae) from Sverdrupfjella, Antarctica, with notes on related species in five genera. *Norwegian Journal of Entomology*, **25**, 15–20.
- Lawrence, P.N. (1978c). Variation in the Palaetropical Collembola species *Cryptopygus fasciatus* with three new synonyms and notes on the subgenus *Rhodanella*. *Revue d'Écologie et de Biologie du Sol*, **15**, 265–71.
- Lawrence, P.N. (1979). Observations on the taxonomy and ecology of *Onychiurus armatus* (Collembola; Onychiuridae) and their wider implications in agriculture and evolution. *Revue d'Écologie et de Biologie du Sol*, **16**, 259–77.
- Lawrence, P.N. (1983). Springtails: Order Collembola. In *Laois – an environmental history* (ed. J. Feehan), pp. 162–5. Ballykilkavan Press, Ballykilkavan, Ireland.

- Lawrence, P.N. and Goto, H.E. (1968). On Bagnall's species of the genera *Anurida* and *Anuridella* (Collembola: Hypogastruridae). *Proceedings of the Royal Entomological Society of London*, **37B**, 16–28.
- Lawrence, P.N. and Khaloyan, O.K. (1977). The taxonomy and ecology of *Proctostephanus madeirensis* Da Gama, 1959 (Collembola) colonising waste tips in Britain. *Entomologist's Gazette*, **28**, 127–32.
- Lawrence, P.N. and Massoud, Z. (1973). Cuticle structures in the Collembola (Insecta). *Revue d'Écologie et de Biologie du Sol*, **10**, 77–101.
- Lawrence, P.N., Gilbert, J.L., and Airy Shaw, H.K. (1967). Additions to the wild fauna and flora of the Royal Botanic Gardens, Kew. XXVIII. A contribution to the Collembolan fauna. *Kew Bulletin*, **21**, 229–39.
- Leather, S.R. (1995). New terms for cold: in support of a re-classification on insect cold hardiness. *Antenna*, **19**, 66–7.
- Leatherdale, D. (1958). A host catalogue of British entomogenous Fungi. *Entomologist's Monthly Magazine*, **94**, 103–5.
- Ledermüller, M.F. (1764). *Amusement microscopique tant pour l'esprit que pour les yeux*. Adam Wolfgang Winterschmidt, Nuremberg.
- Lee, B.H. (1973). Étude de la faune coréenne des insectes Collembolés. I. Liste des Collembolés de Corée et description de trois nouvelles espèces. *Revue d'Écologie et de Biologie du Sol*, **10**, 435–49.
- Lee, B.H. (1974a). Étude de la faune coréenne des insectes Collembolés. II. Description de quatre espèces nouvelles de la famille Hypogastruridae. *Nouvelle Revue d'Entomologie*, **4**, 89–102.
- Lee, B.H. (1974b). Étude de la faune coréenne des insectes Collembolés. III. Description de huit espèces nouvelles de Neanuridae et Onychiuridae. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 3*, **220**, 573–98.
- Lee, B.H. (1974c). Étude de la faune coréenne des insectes Collembolés. V. Inventaire des grottes de Corée et étude sur les Tomoceridae cavernicoles avec la description d'une nouvelle espèce. *Annales de Spéléologie*, **29**, 403–18.
- Lee, B.H. (1975). Étude de la faune coréenne des insectes Collembolés. VI. Sur la famille des Tomoceridae, édaphiques, avec la description de quatre nouvelles espèces et d'une nouvelle sous-espèce. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 3*, **224**, 945–61.
- Lee, B.H. (1977). A study of the Collembola fauna of Korea. IV. The family Isotomidae (Insecta), with description of five new species. *Pacific Insects*, **17**, 155–69.
- Lee, B.H. (1980a). Two neanurid species of Collembola (Insecta) from Korea with polytene chromosomes in salivary glands. *Korean Journal of Zoology*, **13**, 251–62.
- Lee, B.H. (1980b). Polytene chromosomes and salivary glands of *Morulina triverrucosa* (Collembola, Insecta) from Korea. *Commemoration Papers for Professor C.W. Kim's 60th Birthday Anniversary*, 209–17.
- Lee, B.H. (1981). Polytene chromosomes in Neanurid species (Collembola, Insecta) from Korea and their evolutionary implications. *Annual Report of Biological Research, Jeonbuk National University, Jeonju, Korea*, **2**, 19–27.
- Lee, B.H. (1982). A new neanurid species *Lobella daeana* Lee, with polytene chromosomes in salivary gland cells. *Annual Report of Biological Research, Jeonbuk National University, Jeonju, Korea*, **3**, 219–22.
- Lee, B.H. (1983a). A new subfamily Caputaurinae with two new species of Neanurid Collembola from Korea and the evolutionary consideration. *Korean Journal of Entomology*, **13**, 27–36.
- Lee, B.H. (1983b). A new genus of *Tetraloba* of Neanuridae, Collembola from Korea. *Korean Journal of Entomology*, **13**, 37–41.
- Lee, B.H. (1985a). Comparative morphology and cytology of salivary glands in Neanurid Collembola. *Korean Journal of Genetics*, **7**, 177–83.
- Lee, B.H. (1985b). Cladistic analysis of Neanuridae (Collembola) using character weighted and character unweighted approaches. *Korean Journal of Systematic Zoology*, **1**, 3–20.
- Lee, B.H. and Choe, Y.S. (1979). Two new species of *Hypogastrura* with some notes on additional collections of Neanuridae and Tomoceridae. *Korean Journal of Entomology*, **9**, 1–8.
- Lee, B.H. and Kim, J.T. (1984). Eight new species of Korean Pseudachorutinae (Neanuridae, Collembola). *Korean Journal of Entomology*, **14**, 13–23.
- Lee, B.H. and Kim, J.T. (1990). Systematic studies on Chinese Collembola (Insecta). II. Five new species and two new records from Taiwan in the Family Neanuridae. *Korean Journal of Systematic Zoology*, **6**, 235–50.
- Lee, B.H. and Kim, J.T. (1994). Systematic study on some interstitial Collembola (Insecta) from sand dunes of Korean Western coast. *Korean Journal of Systematic Zoology*, **10**, 207–15.
- Lee, B.H. and Kim, J.T. (1995a). Population dynamics of the springtail, *Gulgastrura reticulosa* (Insecta, Collembola) from a Korean cave. *Special Bulletin of the Japanese Society of Coleopterologists, Tokyo*, **4**, 183–8.

- Lee, B.H. and Kim, J.T. (1995b). Two new species of Collembola (Insecta) from Korea. *Korean Journal of Entomology*, **25**, 135–8.
- Lee, B.H. and Lee, W.K. (1981). A taxonomic study of soil microarthropods with reference to *Homidia* (Collembola) and *Oribatei* (Acari). *Annual Report of Biological Research, Jeonbuk National University, Jeonju, Korea*, **2**, 129–40.
- Lee, B.H. and Park, K.H. (1984). Some Entomobryidae including six new species and one cave form (Collembola) from Korea. *Korean Journal of Zoology*, **27**, 177–88.
- Lee, B.H. and Park, K.H. (1986). Three new species of Onychiuridae (Collembola) from a Korean cave. *Korean Journal of Systematic Zoology*, **2**, 11–20.
- Lee, B.H. and Park, K.H. (1989). Systematic studies of Chinese Collembola (Insecta). I. Four new species and three new records of Entomobryidae from Taiwan. *Chinese Journal of Entomology*, **9**, 263–82.
- Lee, B.H. and Park, K.H. (1991). A systematic study of Korean Entomobryidae (Collembola, Insecta) based on cladistic analysis of phenotypic and allozyme data. *Korean Journal of Zoology*, **34**, 265–88.
- Lee, B.H. and Park, K.H. (1992). Collembola from North Korea. II. Entomobryidae and Tomoceridae. *Folia Entomologica Hungarica*, **53**, 93–111.
- Lee, B.H. and Thibaud, J.M. (1975). Étude de la faune coréenne des insectes Collembolés. VII. Hypogastruridae de Corée du Nord. *Nouvelle Revue d'Entomologie*, **1**, 3–11.
- Lee, B.H. and Thibaud, J.M. (1987). A critical review of the taxonomy of *Gulgastrura reticulosa*, a cave springtail from Korea. *Systematic Entomology*, **12**, 73–9.
- Lee, B.H., Kim, B.J., and Kim, J.T. (1993). Collembola from North Korea. III. Isotomidae. *Korean Journal of Systematic Zoology*, **9**, 281–92.
- Lee, R.E. and Baust, J.G. (1981). Seasonal patterns of cold-hardiness in Antarctic terrestrial arthropods. *Comparative Biochemistry and Physiology*, **70A**, 579–82.
- Leetham, J.W. and Milchunas, D.G. (1985). The composition and distribution of soil microarthropods in the shortgrass steppe in relation to soil water, root biomass and grazing by cattle. *Pedobiologia*, **28**, 311–25.
- Leeuwenhoek, A. van (1684–1718). *Werken*. Cornelius Boutesteyn, Leiden.
- Lehmann, U. and Hillmer, G. (1983). *Fossil invertebrates*. Cambridge University Press.
- Leinaas, H.P. (1980). *Isotoma blekeni* n.sp. (Collembola: Isotomidae) from coniferous forest in Norway. Ecological segregation of related, coexisting species. *Revue d'Écologie et de Biologie du Sol*, **17**, 281–9.
- Leinaas, H.P. (1981a). Activity of Arthropoda in snow within a coniferous forest with special reference to Collembola. *Holarctic Ecology*, **4**, 127–38.
- Leinaas, H.P. (1981b). Cyclomorphosis in *Hypogastrura lapponica* (Axelson, 1902) (= *H. frigida* (Axelson, 1905) syn.nov.) (Collembola, Poduridae). Morphological adaptations and selection for winter dispersal. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **19**, 278–85.
- Leinaas, H.P. (1981c). Cyclomorphosis in the furca of the winter active Collembola *Hypogastrura socialis* (Uzel). *Entomologica Scandinavica*, **12**, 35–8.
- Leinaas, H.P. (1983a). Winter strategy of surface dwelling Collembola. *Pedobiologia*, **25**, 235–40.
- Leinaas, H.P. (1983b). Synchronized moulting controlled by communication in group-living Collembola. *Science*, **219**, 193–5.
- Leinaas, H.P. (1988). Anal sacks: an unknown organ in Poduromorpha (Collembola). *Zoologica Scripta*, **17**, 277–84.
- Leinaas, H.P. and Ambrose, W.G. (1992). Utilization of different foraging habitats by the purple sandpiper *Calidris maritima* on a Spitsbergen beach. *Fauna Norvegica*, **15C**, 85–91.
- Leinaas, H.P. and Bleken, E. (1983). Egg diapause and demographic strategy in *Lepidocyrtus lignorum* Fabricius (Collembola; Entomobryidae). *Oecologia*, **58**, 194–9.
- Leinaas, H.P. and Fjellberg, A. (1985). Habitat structure and life history strategies of two partly sympatric and closely related lichen feeding collembolan species. *Oikos*, **44**, 448–58.
- Leinaas, H.P. and Sømme, L. (1984). Adaptations in *Xenylla maritima* and *Anurophorus laricis* (Collembola) to lichen habitats on alpine rocks. *Oikos*, **43**, 197–206.
- Leonard, M.A. (1984). Observations on the influence of culture conditions of the fungal feeding preferences of *Folsomia candida* (Collembola: Isotomidae). *Pedobiologia*, **26**, 361–7.
- Leonard, M.A. and Anderson, J.M. (1991a). Growth dynamics of Collembola (*Folsomia candida*) and a fungus (*Mucor plumbeus*) in relation to nitrogen availability in spatially simple and complex laboratory systems. *Pedobiologia*, **35**, 163–73.
- Leonard, M.J. and Anderson, J.M. (1991b). Grazing interactions between a collembolan and fungi in a leaf litter matrix. *Pedobiologia*, **35**, 239–46.
- Leonard, M.A. and Bradbury, P.C. (1984). Aggregative behaviour in *Folsomia candida* (Collembola: Isotomidae) with respect to previous conditioning. *Pedobiologia*, **26**, 369–72.

- Lescure, J., Jeremie, J., Lourenço, W., Mauries, J.P., Pierre, J., Sastre, C., and Thibaud, J.M. (1991). Biogeographie et insularite: l'exemple des Petits Antilles. *Compte Rendu de la Société Biogéographique*, **67**, 41–59.
- Li, Z. (1992). Two new species of *Neanura* (s.str.) MacGillvray (Collembola: Neanuridae) from China. *Entomotaxonomia*, **13**, 157–60.
- Lin, S.X. and Xia, F. (1985). A new species of *Onychiurus* (Collembola, Onychiuridae). *Acta Entomologica Sinica*, **28**, 80.
- Linnaeus, C. (1735). *Systema naturae* (1st edn). Leydae.
- Linnaeus, C. (1758). *Systema naturae* (10th edn). Holmiae.
- Lister, A., Usher, M.B., and Block, W. (1987). Description and quantification of field attack rates by predatory mites: an example using an electrophoresis method with a species of Antarctic mite. *Oecologia*, **72**, 185–91.
- Lister, A., Block, W., and Usher, M.B. (1988). Arthropod predation in an Antarctic terrestrial community. *Journal of Animal Ecology*, **57**, 957–71.
- Little, C. (1990). *The terrestrial invasion: an ecophysiological approach to the origins of land animals*. Cambridge University Press.
- Lobbess, P.V. (1977). The postembryonic development of the thoracic chaetotaxy of *Protaphorura armata* and *P. furcifera* (Collembola: Onychiuridae). *Bulletin Zoologisch Museum, Universiteit van Amsterdam*, **6**, 31–8.
- Longstaff, B.C. (1976). The dynamics of collembolan populations: competitive relationships in an experimental system. *Canadian Journal of Zoology*, **54**, 948–62.
- Loring, S.J. (1981). Response of *Hypogastrura nivicola* (Collembola, Hypogastruridae) to variable relative humidity. *Pedobiologia*, **22**, 167–71.
- Loring, S.J. (1984). *Janetschkebrya epiphyta*, a new species from Peru (Collembola, Entomobryidae). *Revue d'Ecologie et de Biologie du Sol*, **21**, 563–66.
- Loring, S.J. (1985). Gamma radiation effects on Collembola. *Environmental Entomology*, **14**, 805–9.
- Loring, S.J. and Snider, R.J. (1983). *Sminthurus sagitta*, new species from New Mexico (Collembola: Sminthuridae). *Florida Entomologist*, **66**, 185–91.
- Loring, S.J., Snider, R.J., and Robertson, L.S. (1981). The effects of three tillage practices on Collembola and Acarina populations. *Pedobiologia*, **22**, 172–84.
- Loring, S.J., Weems, D.C., and Whitford, W.G. (1988). Abundance and diversity of surface active Collembola along a watershed in the northern Chihuahuan desert. *American Midland Naturalist*, **119**, 21–30.
- Lübbers, B. (1989). Influence of sewage sludge and heavy metals on the abundance of Collembola on two agricultural soils. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 419–28. University of Siena, Siena.
- Lübbers, B. and Larink, O. (1990). Einfluß von Klärschlammdeponierung und Schwermetallbelastung auf Collembolen im Ackerboden. *Verhandlungen der Gesellschaft für Ökologie*, **19**, 310–15.
- Lubbock, J. (1862a). Notes on the Thysanura. Part I. Sminthuridae. *Transactions of the Linnean Society of London (Zoology)*, **23**, 429–48.
- Lubbock, J. (1862b). Notes on the Thysanura. Part II. Sminthuridae. *Transactions of the Linnean Society of London (Zoology)*, **23**, 589–601.
- Lubbock, J. (1868). Notes on the Thysanura. Part III. *Transactions of the Linnean Society of London (Zoology)*, **26**, 295–304.
- Lubbock, J. (1869). Notes on the Thysanura. Part IV. *Transactions of the Linnean Society of London (Zoology)*, **27**, 277–97.
- Lubbock, J. (1873). *Monograph of the Collembola and Thysanura*. Ray Society, London.
- Lubbock, J. (1898). On some Spitzbergen Collembola. *Journal of the Linnean Society of London (Zoology)*, **26**, 616–19.
- Lubbock, J. (1899). On some Australasian Collembola. *Journal of the Linnean Society of London (Zoology)*, **27**, 334–8.
- Lucianez, M.J. and Simon, J.C. (1988). Estudio colembológico de un robleal y un pinar en la vertiente sur de la Sierra de Gredos. *Eos*, **64**, 57–87.
- Lucianez, M.J. and Simon, J.C. (1989a). Colembolos de prados de la Sierra de Gredos (nota 1). *Boletín del Grupo Entomológico de Madrid*, **4**, 5–16.
- Lucianez, M.J. and Simon, J.C. (1989b). Colembolos del hayedo de Montejo de la Sierra (Madrid). *Actas de Las IX Jornadas, Sevilla, Septiembre 1989*, 102–110.
- Lucianez, M.J. and Simon, J.C. (1991). *Folsomides almanzorensis* sp.n. (Collembola, Isotomidae) de la Sierra de Gredos. *Miscellània Zoològica (Barcelona)*, **15**, 115–19.
- Lucianez, M.J. and Simon, J.C. (1992a). Estudio de la variación estacional de la colembofauna en suelos de alta montaña en la Sierra de Guadarrama (Madrid). *Miscellània Zoològica (Barcelona)*, **15**, 103–13.

- Lucianez, M.J. and Simon, J.C. (1992b). Evolucion de la quetotaxia en *Fissuraphorura gisini* (Collembola: Tullbergiinae). *Redia*, **75**, 157–67.
- Lucianez, M.J. and Simon, J.C. (1992c). Estudio de la ecomorphosis en *Xenylla franzi* en la Sierra de Gredos (Sistema Central, Espana) (Collembola, Hypogastruridae). *Nouvelle Revue d'Entomologie*, **9**, 143–56.
- Lucianez, M.J. and Simon, J.C. (1992d). Un nuevo genero y dos nuevas tribus de Tullbergiinae (Collembola, Onychiuridae) de la Peninsula Iberica. *Eos*, **68**, 105–14.
- Lucianez, M.J. and Simon, J.C. (1992e). *Proisotoma juaniae* nov.sp., nueva especie de colembolo (Collembola, Isotomidae) de suelos del centro de Espana. *Graellsia*, **48**, 87–9.
- Lucianez, M.J. and Simon, J.C. (1993a). Filogenia de los Tullbergiinae Bagnall, 1935 de la Peninsula Iberica (Collembola, Onychiuridae). *Nouvelle Revue d'Entomologie*, **10**, 187–200.
- Lucianez, M.J. and Simon, J.C. (1993b). Vicarianza y distribucion geografica de *Isotomodes bisetosus* e *I. gredensis* (Collembola, Isotomidae) en la Sierra de Gredos (Espana). *Graellsia*, **49**, 51–6.
- Lucianez, M.J. and Simon, J.C. (1994a). Redescription de *Ballistura schoetti* (Dalla Torre, 1895) (Collembola: Isotomidae) y consideraciones sobre su posicion filogenetica. *Boletin de la Asociacion Española de Entomologia*, **18**, 41–8.
- Lucianez, M.J. and Simon, J.C. (1994b). Cinco especies nuevas del genero *Pseudosinella* (Collembola: Entomobryidae) de la Peninsula Iberica. *Annales de la Société Entomologique de France*, N.S., **30**, 319–27.
- Lucianez-Sanchez, M.J., Ruiz-Ortega, M., and Simon-Benito, J.C. (1991). Consideraciones acerca del genero *Paratullbergia* Womersley, 1930 (Collembola, Tullbergiinae) con la descripcion de *P. caroli* nov.sp. *Graellsia*, **47**, 21–8.
- Lucianez, M.J., Martin, J., Perez, M., and Simon, C. (1992). Contribucion al estudio ecologico de la colembofauna en un robledal en la Comunidad de Madrid. In *Historia Natural '91* (ed. A. Alemany), pp. 203–10.
- Lupetti, P., Malatesta, E., and Dallai, R. (1989). Observations on soil fauna activity and on midgut content of Collembola. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 307–15. University of Siena, Siena.
- Lupetti, P., Marsili, L., Focardi, S., and Dallai, R. (1994). Organochlorine compounds in litter-dwelling arthropods: Collembola (Insecta, Apterygota) from Central Italy. *Acta Zoologica Fennica*, **195**, 94–7.
- Lussenhop, J. (1992). Mechanisms of microarthropod-microbial interactions in soil. *Advances in Ecological Research*, **23**, 1–33.
- Lussenhop, J. (1993). Effects of Collembola species on nodule occupancy by two *Bradyrhizobium japonicum* strains. *Soil Biology and Biochemistry*, **25**, 775–80.
- Lussenhop, J. (1996). Collembola as mediators of microbial symbiont effects to soybeans. *Soil Biology and Biochemistry*, **28**, 363–9.
- Lussenhop, J. and Fogel, R. (1995). Observing soil biota in situ. *Geoderma*, **56**, 25–36.
- Lussenhop, J., Fogel, R., and Pregitzer, K. (1991). A new dawn for soil biology: video analysis of root soil microbial faunal interactions. *Agriculture, Ecosystems and Environment*, **34**, 235–49.
- Lyford, W.H. (1975). Overland migration of Collembola (*Hypogastrura nivicola* Fitch) colonies. *American Midland Naturalist*, **94**, 205–9.
- Mackay, D. (1988). On low, very low, and negligible concentrations. *Environmental Toxicology and Chemistry*, **7**, 1–3.
- Mackay, W.P., Silva, S., and Whitford, W.G. (1987). Diurnal activity patterns and vertical migration in desert soil microarthropods. *Pedobiologia*, **30**, 65–71.
- MacLagen, D.S. (1932). A ecological study of the 'Lucerne Flea'. I. and II. *Bulletin of Entomological Research*, **23**, 101–45, 151–90.
- Maclean, S.F., Behan, V., and Fjellberg, A. (1978). Soil Acari and Collembola from Chaun Bay, Northern Chukotka. *Arctic and Alpine Research*, **10**, 559–68.
- Maddox, J.V., Mari Mutt, J.A.M., and Brunjes, V. (1982). Microsporidia from 5 species of entomobryid Collembola. *Journal of Invertebrate Pathology*, **40**, 340–9.
- Maes, J.M., and Palacios-Vargas, J.G. (1988). Catalogo de los insectos Apterygota de Nicaragua. *Rev. Nica. Ent.*, **4**, 1–9.
- Maki, T. (1938). Studies on the thoracic musculature of insects. *Memoirs of the Faculty of Science and Agriculture, Taihoku Imperial University*, **24**, 1–343.
- Malatesta, E., Lupetti, P., and Dallai, R. (1986). Preliminary observations on the soil fauna activity in a *Quercus ilex* wood. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 163–9. University of Siena, Siena.
- Mallow, D., Snider, R.J., and Robertson, L.S. (1985). Effects of different management practices on Collembola and Acarina in corn production systems. II. The effects of moldboard plowing and atrazine. *Pedobiologia*, **28**, 115–31.

- Manier, J.F. and Bouix, G. (1981). Ultrastructural study of *Mantonella podurae* n.sp., coccidia parasitic in *Podura aquatica* Linne (Insect Collembola). *Protistologica*, **17**, 203–14.
- Manton, S.M. (1977). *The arthropods. Habits, functional morphology and evolution*. Clarendon Press, Oxford.
- Margulis, L. (1992). Biodiversity: molecular biological domains, symbiosis and kingdom origins. *BioSystems*, **27**, 39–52.
- Mari Mutt, J.A.M. (1976). The Genera of Collembola (Insecta) in Puerto Rico: keys, diagnoses and general comments. *Journal of Agriculture of the University of Puerto Rico*, **60**, 113–28.
- Mari Mutt, J.A.M. (1977). New species of melittophilous *Pseudocyphoderus* from Costa Rica and remarks on taxonomy (Collembola: Cyphoderidae). *Entomological News*, **88**, 229–34.
- Mari Mutt, J.A.M. (1978a). Swarming of *Entomobrya unostrigata* (Insecta: Collembola) in South Holland, Cook County, Illinois. *Transactions of the Illinois State Academy of Science*, **71**, 236–7.
- Mari Mutt, J.A.M. (1978b). *The types of Collembola (Insecta) at the Illinois Natural History Survey*. Illinois Natural History Survey, Biological notes No. 103. Department of Registration and Education, Natural History Survey Division, Urbana, Illinois.
- Mari Mutt, J.A.M. (1978c). A review of the genus *Mastigoceras* with remarks on its systematic position (Collembola: Entomobryidae). *Pan Pacific Entomologist*, **54**, 43–7.
- Mari Mutt, J.A.M. (1979a). A review of the genus *Dicranocentrus* Schött (Insecta: Collembola: Entomobryidae). *Bulletin of the University of Puerto Rico*, **259**, 1–79.
- Mari Mutt, J.A.M. (1979b). A review of the genus *Uchidanura* with description of a new species (Collembola: Neanuridae). *Pacific Insects*, **20**, 53–8.
- Mari Mutt, J.A.M. (1980). A classification of the Orchesellinae with a key to the tribes, genera and subgenera (Collembola, Entomobryidae). *Annals of the Entomological Society of America*, **73**, 455–9.
- Mari Mutt, J.A.M. (1981a). Two new *Dicranocentrus* from Nepal and a key to the Indian and Nepalese species (Collembola, Entomobryidae). *Pan Pacific Entomologist*, **57**, 493–9.
- Mari Mutt, J.A.M. (1981b). New genus, a new species and complements to the descriptions of 7 neotropical *Dicranocentrus* (Collembola, Entomobryidae, Orchesellinae). *Journal of Agriculture of the University of Puerto Rico*, **65**, 90–107.
- Mari Mutt, J.A.M. (1981c). A new species and complements to the descriptions of 9 African or oriental *Dicranocentrus* (Collembola, Entomobryidae). *Journal of Agriculture of the University of Puerto Rico*, **65**, 160–70.
- Mari Mutt, J.A.M. (1981d). Redescription of *Willowsia jacobsoni* (Börner), an entomobryid with conspicuous sexual dimorphism (Insecta: Collembola). *Journal of Agriculture of the University of Puerto Rico*, **65**, 361–73.
- Mari Mutt, J.A.M. (1982). A new species of *Heteromurus* (*Alloscopus*) from Papua New Guinea and descriptive notes on the other species of the subgenus (Collembola, Entomobryidae, Orchesellinae). *Pacific Insects*, **24**, 84–94.
- Mari Mutt, J.A.M. (1983a). Four new species of *Dicranocentrus* and *Heteromurus* from the state of Merida, Venezuela (Collembola, Entomobryidae). *Journal of Agriculture of the University of Puerto Rico*, **67**, 148–64.
- Mari Mutt, J.A.M. (1983b). Collembola in amber from the Dominican Republic. *Proceedings of the Entomological Society of Washington*, **85**, 575–87.
- Mari Mutt, J.A.M. (1983c). Three new species of *Orchesellides* from North Korea (Collembola, Entomobryidae, Orchesellinae). *International Journal of Entomology*, **25**, 297–309.
- Mari Mutt, J.A.M. (1984a). New records for *Corynothrix borealis* and a study of its variability (Collembola, Entomobryidae, Orchesellinae). *International Journal of Entomology*, **26**, 369–77.
- Mari Mutt, J.A.M. (1984b). Five new species of Orchesellini from Central Mexico (Collembola: Entomobryidae: Orchesellinae). *Proceedings of the Entomological Society of Washington*, **86**, 808–20.
- Mari Mutt, J.A.M. (1985a). Three new species of *Heteromurus* (*Alloscopus*) and descriptive notes for species of the subgenus (Collembola, Entomobryidae). *Florida Entomologist*, **68**, 335–46.
- Mari Mutt, J.A.M. (1985b). A new species of *Orchesella* from Manitoba, Canada (Collembola: Entomobryidae). *Pan Pacific Entomologist*, **61**, 50–3.
- Mari Mutt, J.A.M. (1985c). A new species of *Heteromurus* from Puerto Rico (Collembola, Entomobryidae). *Entomological News*, **96**, 145–7.
- Mari Mutt, J.A.M. (1985d). Eight new species of *Dicranocentrus* and redescrptions for *Dicranocentrus thaicus* and *Dicranocentrus pilosus* (Collembola, Entomobryidae, Orchesellinae). *Journal of Agriculture of the University of Puerto Rico*, **69**, 297–322.
- Mari Mutt, J.A.M. (1986). Puerto Rican species of *Lepidocyrtus* and *Pseudosinella* (Collembola: Entomobryidae). *Caribbean Journal of Science*, **22**, 1–48.

- Mari Mutt, J.A.M. (1987a). Redescription of *Seira oceanica* Yosii 1960 (Collembola, Entomobryidae). *Journal of Agriculture of the University of Puerto Rico*, **71**, 331–3.
- Mari Mutt, J.A.M. (1987b). A new *Seira* from the United States with a redescription of *Seira bipunctata* (Packard) and new records for *Seira distincta* Mari Mutt (Collembola, Entomobryidae). *Proceedings of the Entomological Society of Washington*, **89**, 126–31.
- Mari Mutt, J.A.M. (1987c). Two new species of *Heteromurus* from Sulawesi Utara (Celebes) and a new record for *Heteromurus tenuicornis* Börner (Collembola, Entomobryidae). *Journal of the New York Entomological Society*, **95**, 572–6.
- Mari Mutt, J.A.M. (1988). A new *Dicranocentrus* from Thailand, redescription of *Dicranocentrus fasciatus* Yosii and records for two other species of Orchesellinae (Collembola, Entomobryidae). *Journal of the Kansas Entomological Society*, **61**, 179–85.
- Mari Mutt, J.A.M. and Bellinger, P.F. (1990). *Catalogue of the Neotropical Collembola*. Flora and Fauna Handbooks Number 5. Sandhill Crane Press, Gainesville, Florida.
- Mari Mutt, J.A.M. and Greenslade, P. (1985). A revision of the genus *Australotomurus* (Collembola: Entomobryidae: Orchesellinae). *Australian Journal of Zoology*, **33**, 217–43.
- Mari Mutt, J.A.M. and Gruia, M.M. (1983). A revision of the genus *Metasinelia* Denis (Collembola, Entomobryidae). *Journal of Agriculture of the University of Puerto Rico*, **67**, 121–47.
- Mari Mutt, J.A.M. and Palacios-Vargas, J.G. (1987). *Americabrya*, a new genus of Entomobryidae (Collembola), with a redescription of *A. arida* (Christiansen and Bellinger) based on Mexican specimens and descriptive notes for *A. epiphyta* (Loring). *Journal of the New York Entomological Society*, **95**, 99–108.
- Mari Mutt, J.A.M. and Soto-Adames, F.N. (1987). Molting, fecundity, and longevity in *Willowsia jacobsoni* (Collembola: Entomobryidae). *Caribbean Journal of Science*, **23**, 298–304.
- Marinissen, J.C.Y. and Bok, J. (1988). Earthworm-amended soil structure: its influence on Collembola populations in grassland. *Pedobiologia*, **32**, 243–52.
- Maroni, G., Wise, J., Young, J.E., and Otto, E. (1987). Metallothionein gene duplications and metal tolerance in natural populations of *Drosophila melanogaster*. *Genetics*, **117**, 739–44.
- Marques, M.D., Cutkomp, L.K., Cornelissen, G., Marques, N., and Halberg, F. (1987). Lifespan of springtail on the 12-h shifts at varying intervals of 12-hourly alternation in ambient temperature. In *Advances in chronobiology*, Part A., pp. 257–64. Alan R. Liss, New York.
- Marques, M.D., Cornelissen, G., Cutkomp, L.K., Halberg, F., and Marques, N. (1988). Experimental models for the study of chronimmunomodulation (rhythms of the springtail *Folsomia candida*, Collembola: Isotomidae). *Chronobiologia*, **15**, 183–9.
- Marshall, C.R., Raff, E.C., and Raff, R.A. (1994). Dollo's law and the death and resurrection of genes. *Proceedings of the National Academy of Sciences of the United States of America*, **91**, 12283–7.
- Marshall, V.G. (1978). Gut content analysis of the collembolan *Bourletiella hortensis* (Fitch) from a forest nursery. *Revue d'Écologie et de Biologie du Sol*, **15**, 243–50.
- Marshall, V.G. and Illytzyk, S. (1976). Evaluation of chemically controlling the collembolan *Bourletiella hortensis* on germinating Sitka spruce and western hemlock in the nursery. *Canadian Journal of Forest Research*, **6**, 467–74.
- Marshall, V.G. and Kevan, K.M. (1962). Preliminary observations on the biology of *Folsomia candida* Willem, 1902 (Collembola: Isotomidae). *Canadian Entomologist*, **94**, 575–86.
- Marshall, V.G., Shrimpton, G.M., and Battigelli, J.P. (1990). A preliminary survey of Collembola in forest nurseries of British Columbia. *Journal of the Entomological Society of British Columbia*, **87**, 85–9.
- Martynova, E.F. (1964). Order Podura (Collembola). In *Keys to the insects of the European USSR, Volume 1. Apterygota, Palaeoptera, Hemimetabola*. Keys to the fauna of the USSR, No. 84. Akademiya Nauk SSSR Zoologicheskii Institut. Israel Program for Scientific Translations, Jerusalem, 1967.
- Martynova, E.F. (1967). On diagnostics of certain species of springtails of the genera *Folsomia* Willem and *Pseudofolsomia*, gen.n. (Collembola, Isotomidae), recorded from Middle Volga region. *Revue d'Entomologie de l'URSS*, **46**, 845–9.
- Martynova, E.F. (1971). New species of springtails (Collembola) from mountain and steppe regions of the USSR. *Revue d'Entomologie de l'URSS*, **50**, 598–611.
- Martynova, E.F. (1978). *Uralaphorura*, a new name for *Uralia* Martynova, 1976 (Collembola: Onychiuridae). *Entomologische Berichten*, **38**, 63.
- Martynova, E.F. (1979). A new species of springtail (Collembola, Onychiuridae) from the South of Primorye territory. *Revue d'Entomologie de l'URSS*, **58**, 799–806.
- Massoud, Z. (1964a). Description d'un nouveau genre de poduromorphe (Collembola Arthropleona). *Revue d'Écologie et de Biologie du Sol*, **1**, 511–18.
- Massoud, Z. (1964b). Collembolles poduromorphes de l'Angola récoltés par A. de Barros Machado. *Publicações Culturais Companhia de Diamantes de Angola*, **25**, 55–72.

- Massoud, Z. (1967a). Contribution à l'étude de *Rhyniella praecursor* Hirst et Maulik 1926, Collembole fossile du Dévonien. *Revue d'Écologie et de Biologie du Sol*, **4**, 497–505.
- Massoud, Z. (1967b). Monographie des Neanuridae, Collembolles Poduromorphes à pièces buccales modifiées. In *Biologie d'Amerique et Australie*, Vol. III, pp. 1–399. CNRS, Paris.
- Massoud, Z. (1969). Étude de l'ornementation épicuticulaire du tégument des Collembolles au microscope électronique à balayage. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **268**, 1407–9.
- Massoud, Z. (1971). Contribution à la connaissance morphologique et systématique des Collembolles Neelidae. *Revue d'Écologie et de Biologie du Sol*, **8**, 195–8.
- Massoud, Z. (1976). Essai de synthèse sur la phylogénie des Collembolles. *Revue d'Écologie et de Biologie du Sol*, **13**, 241–52.
- Massoud, Z. and Barra, J.A. (1980). Interprétation ultrastructurale de la microsculpture epicuticulaire des Collembolles Entomobryomorpha (Aptérygotes). *Revue d'Écologie et de Biologie du Sol*, **17**, 251–60.
- Massoud, Z. and Bellinger, P.F. (1963). Les Collembolles de la Jamaïque. II. *Bulletin de la Société Zoologique de France*, **88**, 448–61.
- Massoud, Z. and Betsch, J.M. (1966a). Description de la nouvelle lignée de Collembolles Entomobryomorpha: Microfalculinae Massoud et Betsch. *Revue d'Écologie et de Biologie du Sol*, **3**, 571–84.
- Massoud, Z. and Betsch, J.M. (1966b). Description d'une nouvelle lignée de Collembolles Entomobryomorpha récoltée à Madagascar. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **263**, 733–5.
- Massoud, Z. and Betsch, J.M. (1966c). Considérations sur l'antenne des Sminthurinae et description de deux nouvelles espèces de Collembolles interstitiels du genre *Sminthurides* Boerner 1900 (Symphypléones). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 2*, **38**, 574–85.
- Massoud, Z. and Betsch, J.M. (1970). Premiers éléments sur l'étude du dimorphisme sexuel affectant les antennes des Sminthurinae (Collembolles Symphypléones) au microscope électronique à balayage. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **270**, 90–2.
- Massoud, Z. and Betsch, J.M. (1972). Étude sur les Insectes Collembolles. II. Les caractères sexuels secondaires des antennes des Symphypléones. *Revue d'Écologie et de Biologie du Sol*, **9**, 55–97.
- Massoud, Z. and Betsch, J.M. (1973). Existence d'un troisième niveau d'organisation de l'ornementation épicuticulaire chez le Collembole *Tetrodontophora* Reuter 1882. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **276**, 989–90.
- Massoud, Z. and Betsch-Pinot, M.C. (1974). Observations sur la ponte de *Proisotoma minuta* (Collembolles, Isotomidae). *Pedobiologia*, **14**, 208–12.
- Massoud, Z. and Delamare Deboutteville, C. (1964). Révision du genre *Bovicornia* Delamare (Collembole, Symphypléone). *Revue d'Écologie et de Biologie du Sol*, **1**, 519–32.
- Massoud, Z. and Delamare Deboutteville, C. (1969). Étude de l'organisation sensorielle de l'antenne des Neelidae (Collembolles) au microscope électronique à balayage. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **269**, 2554–6.
- Massoud, Z. and Ellis, W.N. (1974). Considérations sur les genres *Tomocerus* et *Pogonognathellus* (Collembola, Insecta). *Pedobiologia*, **14**, 292–9.
- Massoud, Z. and Ellis, W.N. (1977). Proposition pour une classification et une nomenclature cohérente des phanères des Collembolles européens. *Revue d'Écologie et de Biologie du Sol*, **14**, 163–79.
- Massoud, Z. and Najt, J. (1974). Existence de caractères sexuels secondaires chez certains Brachystomellinae (Insectes, Collembolles). *Revue d'Écologie et de Biologie du Sol*, **11**, 553–60.
- Massoud, Z. and Najt, J. (1975). Essais d'interprétation du dimorphisme sexuel chez les Collembolles Brachystomellinae. *Revue d'Écologie et de Biologie du Sol*, **12**, 459–72.
- Massoud, Z. and Najt, J. (1976). Importance des techniques pour l'étude du régime alimentaire des Collembolles. *Revue d'Écologie et de Biologie du Sol*, **13**, 147–53.
- Massoud, Z. and Pinot, M.C. (1973). Comportement de ponte chez les Collembolles *Arrhopalites* Börner. *Revue d'Écologie et de Biologie du Sol*, **10**, 197–210.
- Massoud, Z. and Thibaud, J.M. (1973). Étude comparative de la chétotaxie des insectes collembolles épigés et cavernicoles. *Annales de Spéléologie*, **28**, 331–5.
- Massoud, Z. and Thibaud, J.M. (1977). Essai de classification des Collembolles 'cavernicoles' européens. In *Proceedings of the 6th International Congress of Speleology 1977, Volume 5* (ed. V. Panos), pp. 141–57. Czechoslovak Academy, Prague.
- Massoud, Z. and Thibaud, J.M. (1979). Discussion sur l'hétérogénéité de l'ornementation épicuticulaire chez les *Xenylla* (Collembolles, Hypogastruridae). *Revue d'Écologie et de Biologie du Sol*, **16**, 535–9.
- Massoud, Z. and Thibaud, J.M. (1980). Les Collembolles des Petites Antilles. II. Neanuridae. *Revue d'Écologie et de Biologie du Sol*, **17**, 591–605.

- Massoud, Z. and Thibaud, J.M. (1985). Recherche sur la faune interstitielle aérienne des sables fins: Les Collemboles. *Annales de la Société Entomologique de France*, N.S., **21**, 39–44.
- Massoud, Z. and Thibaud, J.M. (1987). Les Collemboles des Petites Antilles. IV. Neanuridae (suite et fin). *Revue d'Écologie et de Biologie du Sol*, **24**, 91–8.
- Massoud, Z. and Vannier, G. (1965a). Présence de sécrétions cireuses chez les Collemboles. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **260**, 4819–20.
- Massoud, Z. and Vannier, G. (1965b). *Megalothorax gabonicus*, n.sp. et discussion sur la griffe des Neelidae. *Revue d'Écologie et de Biologie du Sol*, **2**, 229–37.
- Massoud, Z. and Vannier, G. (1967). Révision du genre *Neelus* Folsom 1896 (Collembola) et description de *Neelus labralisetosus* n.sp. des Iles Salomon. *Revue d'Écologie et de Biologie du Sol*, **4**, 625–37.
- Massoud, Z., Poinso, N., and Poivre, C. (1968). Contribution à l'étude du comportement constructeur chez les Collemboles. *Revue d'Écologie et de Biologie du Sol*, **5**, 283–6.
- Massoud, Z., Najt, J., and Thibaud, J.M. (1975). Description d'un nouveau genre de Collembola de la Jamaïque. Considérations sur le labium des Arthropléones. *Nouvelle Revue d'Entomologie*, **2**, 111–17.
- Massoud, Z., Ellis, W., and Munsch, A. (1977). Proposition pour une classification et une nomenclature cohérente des phanères des Collemboles européens. *Revue d'Écologie et de Biologie du Sol*, **14**, 163–79.
- Massoud, Z., Thibaud, J.M., Cancela da Fonseca, J.P., and Dolin, M. (1983). Périodicité d'échantillonnage et perte d'information dans l'estimation de la densité des populations d'insectes Collemboles. *Pedobiologia*, **25**, 325–30.
- Massoud, Z., Betsch, J.M., and Thibaud, J.M. (1984). Expérience de piétinement contrôlé du sol d'une forêt périurbaine: effets sur le peuplement de Collemboles. *Revue d'Écologie et de Biologie du Sol*, **21**, 507–18.
- Mateos, E. (1988). Ecología de los colembolos (Collembola, Insecta) edáficos del encinar montano del Montseny (Barcelona). *Miscellània Zoològica (Barcelona)*, **12**, 97–107.
- Mateos, E. (1991). Diversidad de las comunidades de colémbolos en suelos de encinar mediterráneo. *Studio Oecologia (Salamanca)*, **8**, 219–31.
- Mateos, E. (1992). Las poblaciones de *Mesaphorura italica* Rusek, 1971 en suelos de encinar mediterráneo. *Actas V Congreso Ibérico de Entomología*, Vol. II, 299–310.
- Mateos, E. (1993). *Pseudosinella subiliciensis* n.sp., une nueva especie de *Pseudosinella* (Collembola, Entomobryidae) edáfica del noreste Iberico (Catalunya, Espana). *Graellsia*, **49**, 87–90.
- Mateos, E. and Arbea, J.I. (1986). Dos nuevas especies de *Protaphorura* del grupo *memorata* (Collembola, Onychiuridae) del macizo del Montseny (Barcelona). *Actas de Las VIII Jornadas A e E, Sevilla*, 281–9.
- Mateos, E. and Selga, D. (1991). Efecto de los incendios forestales sobre las poblaciones de colémbolos edáficos en bosque mediterráneo. *Revue d'Écologie et de Biologie du Sol*, **28**, 19–30.
- Mathes, K. and Weidemann, G. (1990). A baseline-ecosystem approach to the analysis of ecotoxicological effects. *Ecotoxicology and Environmental Safety*, **20**, 197–202.
- Matic, R. and Koledin, D. (1985). Preference and feeding specificity of *Tetrodontophora bielanensis* (Collembola: Insecta) under laboratory conditions. *Revue d'Écologie et de Biologie du Sol*, **22**, 121–9.
- Matsuzaki, M. (1973). Oogenesis in the springtail *Tomocerus minutus* Tullberg (Collembola: Tomoceridae). *International Journal of Insect Morphology and Embryology*, **2**, 335–49.
- May, R.M. (1994). Conceptual aspects of the quantification of the extent of biological diversity. *Philosophical Transactions of the Royal Society of London*, **345B**, 13–20.
- Maynard, E.A. (1951). *A monograph of the Collembola or springtail insects of New York State*. Comstock, Ithaca, New York.
- Mayr, E. (1940). Speciation phenomena in birds. *American Naturalist*, **74**, 249–78.
- McClachlan, R. (1869). Swarming of *Anurida tuberculata* on the surface of a pond. *Proceedings of the Entomological Society of London for the Year 1869*, p. xiii.
- McMillan, J.H. (1975). Interspecific and seasonal analysis of the gut contents of three Collembola (Family Onychiuridae). *Revue d'Écologie et de Biologie du Sol*, **12**, 449–57.
- McMillan, J.H. (1976). Laboratory observations on the food preference of *Onychiurus armatus* (Tullb.) Gisin (Collembola: Onychiuridae). *Revue d'Écologie et de Biologie du Sol*, **13**, 353–64.
- McMillan, J.H. and Healey, I.N. (1971). A quantitative technique for the analysis of the gut contents of Collembola. *Revue d'Écologie et de Biologie du Sol*, **8**, 295–300.
- Meier, P., Suter, E., and Zettel, J. (1988). Cold hardiness strategies of two subalpine springtails. *Cryo Letters*, **9**, 436.
- Mendonça, C. (1990). Duas novas espécies Brasileiras de *Isotomurus* Boerner, 1903 (Collembola: Isotomidae). *Revista Brasileira de Biologia*, **50**, 453–62.
- Mendonça, C. and Arlé, R. (1987). Nova espécie de *Arlea* Womersley 1939 (Collembola: Isotomidae). *Boletim Museu Nacional Rio de Janeiro, Zoologia*, **31**, 1–7.

- Mendonça, C. and Arlé, R. (1992). Variacao quetotaxia em *Brachystomella agrosa* Wray 1953 (Collembola: Neanuridae). *Boletim Museu Nacional Rio de Janeiro, Zoologia*, **35**, 1–9.
- Mendonça, C. and Dosreis, S.F. (1991). Multivariate morphometric analysis of selected *Proisotoma* species (Collembola, Isotomidae). *Zoologischer Anzeiger*, **227**, 98–103.
- Mertens, J. and Blancquaert, J.P. (1980). Population dynamics of *Orchesella cincta* (Collembola) in experimental conditions. *Pedobiologia*, **20**, 301–8.
- Mertens, J. and Bourgoigne, R. (1977). Aggregation pheromone in *Hypogastrura viatica*. *Behavioral Ecology and Sociobiology*, **2**, 44–8.
- Mertens, J., Blancquaert, J.P., and Bourgoigne, R. (1979). Aggregation pheromone in *Orchesella cincta*. *Revue d'Écologie et de Biologie du Sol*, **16**, 441–7.
- Mertens, J., Coessens, R., and Blancquaert, J.P. (1982). Population structure of *Orchesella cincta* (Collembola) in the field based on in situ determination. *Pedobiologia*, **23**, 9–20.
- Mertens, J., Coessens, R., and Blancquaert, J.P. (1983). Reproduction and development of *Hypogastrura viatica* in relation to temperature and submerged condition. *Revue d'Écologie et de Biologie du Sol*, **20**, 567–77.
- Metz, L.J. and Farrier, M.H. (1973). Prescribed burning and populations of soil mesofauna. *Environmental Entomology*, **2**, 433–40.
- Miles, P.M. (1971). Nematodes associated with *Orchesella villosa* (Geoff.) (Collembola, Entomobryidae). *Entomologist's Monthly Magazine*, **107**, 193–4.
- Miles, P.M. (1974). A nematode parasite of *Onychiurus armatus* (Tullberg) (Collembola, Onychiuridae). *Entomologist's Gazette*, **25**, 31–4.
- Miles, P.M. (1975). Springtails (Collembola, Arthropleona) collected by the late Rev. Professor L.W. Grensted, M.A., D.D., F.R.E.S. *Entomologist's Gazette*, **26**, 44–6.
- Miles, P.M. (1976). A phoretic larval *Cheilobus* sp. (Nematoda) and a proturan ectoparasite on Isotomidae (Collembola) also *Howardula* sp. (Nematoda) parasitic on *Parasiticus* sp. (Acari). *Entomologist's Monthly Magazine*, **112**, 169–72.
- Miles, P.M. (1994). Ecomorphosis in Collembola in Wales. *Entomologist's Monthly Magazine*, **130**, 47–8.
- Miller, J.S. and Wenzel, J.W. (1995). Ecological characters and phylogeny. *Annual Review of Entomology*, **40**, 389–415.
- Mills, H.B. (1934). *A monograph of the Collembola of Iowa*. Collegiate Press, Ames, Iowa.
- Mills, J.T. and Sinha, R.N. (1971). Interactions between a springtail, *Hypogastrura tullbergi*, and soil-borne fungi. *Journal of Economic Entomology*, **64**, 398–401.
- Milne, S. (1960). Studies on the life histories of various species of Arthropleone Collembola. *Proceedings of the Royal Entomological Society of London*, **35A**, 133–40.
- Milne, S. (1962). Phenology of a natural population of soil Collembola. *Pedobiologia*, **2**, 41–52.
- Minelli, A. (1993). *Biological systematics. The state of the art*. Chapman and Hall, London.
- Miranda-Rangel, A. and Palacios-Vargas, J.G. (1992). Estudio comparativo de las comunidades de colembolos edáficos de bosque de *Abies religiosa* y cultivo de haba (*Vicia faba*). *Agrociencia (Proteccion Vegetal)*, **3**, (3), 7–18.
- Mitra, S.K. (1972). An accessory ocular structure in two genera of Paronellinae (Collembola: Entomobryidae). *Oriental Insects*, **6**, 267–72.
- Mitra, S.K. (1973). A revision of *Salina* MacGillivray, 1894 (Collembola: Entomobryidae) from India. *Oriental Insects*, **7**, 159–202.
- Mitra, S.K. (1974). A critical study on some species of *Callyntura* Börner, 1906 (Collembola, Entomobryidae, Paronellinae) from India. *Revue d'Écologie et de Biologie du Sol*, **11**, 397–439.
- Mitra, S.K. and Dallai, R. (1980). Studies of the genus *Campylothorax* Schött, 1893 (Collembola, Entomobryidae, Paronellinae) with the description of a new species from Zaire. *Monitore Zoologico Italiano*, (N.S.), Supplemento, **13**, 273–321.
- Moen, P. and Ellis, W.N. (1984). Morphology and taxonomic position of *Podura aquatica* (Collembola). *Entomologia Generalis*, **9**, 193–204.
- Mola, L., Sabatini, M.A., Fratello, B., and Bertolani, R. (1987). Effects of atrazine on two species of Collembola (Onychiuridae) in laboratory tests. *Pedobiologia*, **30**, 145–9.
- Moon, H.P. and Gough, H.J. (1972). Nocturnal activities of two species of *Entomobrya* (Collembola: Entomobryidae) in a difficult environment. *Entomologist's Monthly Magazine*, **108**, 232–3.
- Moore, F.R. and Luxton, M. (1988). The distribution of Collembola on a coal shale heap. *Pedobiologia*, **31**, 157–68.
- Moore, J.C. (1988). The influence of microarthropods on symbiotic and non-symbiotic mutualism in detrital based below ground food webs. *Agriculture, Ecosystems and Environment*, **24**, 147–59.

- Moore, J.C., Snider, R.J., and Robertson, L.S. (1984). Effects of different management practices on Collembola and Acari in corn production systems. I. The effects of no-tillage and atrazine. *Pedobiologia*, **26**, 143–52.
- Moore, J.C., St. John, T.V., and Coleman, D.C. (1985). Ingestion of vesicular-arbuscular mycorrhizal hyphae and spores by soil microarthropods. *Ecology*, **66**, 1979–81.
- Moore, J.C., Ingham, E.R., and Coleman, D.C. (1987). Inter and intraspecific feeding selectivity of *Folsomia candida* (Willem) (Collembola, Isotomidae) on fungi. *Biology and Fertility of Soils*, **5**, 6–12.
- Moore, J.C., Walter, D.E., Hunt, H.W. (1988). Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. *Annual Review of Entomology*, **33**, 419–39.
- Morris, H.M. (1922). The insects and other invertebrate fauna of arable land in Rothamsted. Part I. *Annals of Applied Biology*, **9**, 282–305.
- Morris, H.M. (1927). The insects and other invertebrate fauna of arable land in Rothamsted. Part II. *Annals of Applied Biology*, **14**, 442–64.
- Mouffet, T. (1634). *Insectorum sive minimorum animalium theatrum: olim ab Edoardo Wottono, Conrad Gesnero, Thomaque Pennio inchoatum*. Thomas Cotes, London.
- Mukherjee, P. and Banerjee, S. (1993). Studies on the relation between soil factors and its collembolan fauna (Insecta) of Tiger Hill, Darjeeling. *Journal of Environmental Biology*, **14**, 143–52.
- Müller, O.F. (1776). *Zoologiae Danicae prodromus*. Havniae (Collembola on pp. 183–4).
- Muralledharan, V. and Prabhoo, N.R. (1978). Observations on the feeding habits of some soil Collembola from an abandoned field in Kerala. *Entomon*, **3**, 207–13.
- Murphy, D.H. (1971). Revision of the tropical marine littoral genus *Pseudanurida* Schött (Collembola: Pseudachorutinae). *Pacific Insects*, **13**, 49–63.
- Murray, A. (1877). *Economic entomology, Aptera*. Chapman and Hall, London.
- Muzzio, S.F. (1984). *Neosminthurus bellingeri*, a new species from California (Collembola, Sminthuridae). *Pan Pacific Entomologist*, **60**, 258–63.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., and Woodfin, R.W. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734–7.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., and Woodfin, R.W. (1995). Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of the Royal Society of London*, **347B**, 249–62.
- Najt, J. (1980). Le problème de l'écomorphose dans le genre *Folsomia*. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **116**, 311–20.
- Najt, J. (1983). Modifications morphologiques liées à l'écomorphose chez les Collembolles Isotomidae. *Pedobiologia*, **25**, 337–48.
- Najt, J. (1988). Un nouveau genre de collembolle Brachystomellinae du Chili. *Nouvelle Revue d'Entomologie*, **5**, 205–8.
- Najt, J. and Massoud, Z. (1976). Déformations morphologiques et étude des cas tératologiques chez les Collembolles. *Revue d'Écologie et de Biologie du Sol*, **13**, 205–18.
- Najt, J. and Palacios-Vargas, J.G. (1986). Nuevos Brachystomellinae de México (Collembola, Neanuridae). *Nouvelle Revue d'Entomologie*, **3**, 457–71.
- Najt, J. and Thibaud, J.M. (1987). Collembolles (Insecta) de l'Équateur. I. Hypogastruridae, Neanuridae et Isotomidae. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **9A**, 201–9.
- Najt, J. and Thibaud, J.M. (1988). Collembolles Poduromorpha de Nouvelle-Calédonie. 3. Deux espèces nouvelles de *Brachystomella* (Neanuridae, Brachystomellinae). *Mémoires du Muséum National d'Histoire Naturelle*, **142A**, 33–7.
- Najt, J. and Weiner, W.M. (1985). North Korean Collembola. 6. The genera *Micranurida* Börner and *Philotella* n.g. *Annales de la Société Entomologique de France*, **21**, 29–38.
- Najt, J. and Weiner, W.M. (1991). Collembola Poduromorpha épiédaphiques de la Reserve de la Rivière Bleue, Nouvelle-Calédonie. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **13A**, 97–112.
- Najt, J. and Weiner, W.M. (1992). *Koreanurina* new genus, *Leenurina* new genus and *Caputanurina* Lee, 1983 (Collembola: Neanuridae) from North Korea. *Pan Pacific Entomologist*, **68**, 200–15.
- Najt, J., Dalens, H., and Deharveng, L. (1984). Note sur la biologie, le polymorphisme et le statut taxonomique de quelques populations d'*Hypogastrura* du sous-groupe *tullbergi*. *Revue d'Écologie et de Biologie du Sol*, **21**, 395–413.
- Najt, J., Thibaud, J.M., and Mari Mutt, J.A.M. (1988). Collembolles (Insecta) de l'Équateur. III. Entomobryidae: Orchesellinae. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **10A**, 553–61.
- Najt, J., Thibaud, J.M., and Weiner, W.M. (1990). Collembolles (Insecta) Poduromorphes de Guyane française. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **12A**, 95–121.

- Najt, J., Thibaud, J.M., and Jacquemart, S. (1991). Les Collemboles (Insecta) de l'Archipel des Galápagos. I. Poduromorpha. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie*, **61**, 149–66.
- Nakamura, Y. (1984). Aspects of colonization by *Enchytraeus albidus* (Enchytraeidae) and *Sinella curviseta* (Collembola) in Niimi waste water treatment trench. *Pedobiologia*, **26**, 381–6.
- Nakamura, Y., Itakura, J., and Matsuzaki, I. (1991a). Mycophagous meso soil animals from cropfields in Fukushima Pref. *Edaphologia*, **45**, 49–54.
- Nakamura, Y., Matsuzaki, I., and Itakura, J. (1991b). Effects of mycophagous Collembola on *Rhizoctonia solani* Kühn causing radish, cucumber, cabbage and burdock seedling diseases. *Edaphologia*, **47**, 41–5.
- Nakamura, Y., Matsuzaki, I., and Itakura, J. (1992). Effect of grazing by *Sinella curviseta* (Collembola) on *Fusarium oxysporum* f.sp. *cucumerinum* causing cucumber disease. *Pedobiologia*, **36**, 168–71.
- Natuhara, Y., Imai, C., and Takeda, H. (1994). Classification and ordination of communities of soil arthropods in an urban park of Osaka City. *Ecological Research*, **9**, 131–41.
- Nayrolles, P. (1987). Description de deux nouvelles espèces de *Prorastriopes* (Collembola Symphypléones). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **123**, 123–6.
- Nayrolles, P. (1988). Chétotaxie tibiotarsale des Collemboles Symphypléones. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **5**, (4), 1–19.
- Nayrolles, P. (1989a). Description de deux nouvelles espèces de *Ptenothrix* (Collemboles Symphypléones). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **125**, 105–9.
- Nayrolles, P. (1989b). Données nouvelles sur l'évolution ontogénétique des Collemboles Symphypléones. *Nouvelle Revue d'Entomologie*, **6**, 231–44.
- Nayrolles, P. (1990a). Chétotaxie de la base de la patte des Collemboles Symphypléones. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **6**, (2), 1–26.
- Nayrolles, P. (1990b). Chétotaxie furcale des Collemboles Symphypléones. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **6**, (2), 27–50.
- Nayrolles, P. (1990c). Fauna of Thai caves. III. Two new cavernicolous species of *Arrhopalites* from Thailand (Insecta: Collembola). *Bishop Museum Occasional Papers*, **30**, 288–93.
- Nayrolles, P. (1990d). Chétotaxie d'une nouvelle espèce de *Spatulosminthurus* (Collemboles, Symphypléones). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **126**, 65–71.
- Nayrolles, P. (1991). Le chétotaxie antennaire des Collemboles Symphypléones. *Travaux du Laboratoire d'Ecobiologie des Arthropodes Édaphiques, Toulouse*, **6**, (3), 1–94.
- Nayrolles, P. (1992). Aspects structuraux de la chétotaxie appendiculaire des Collemboles Symphypléones. *Nouvelle Revue d'Entomologie*, **9**, 345–56.
- Nayrolles, P. (1993a). La biométrie des caractères discontinus d'après le revêtement appendiculaire des Collemboles Symphypléones. I. Sur quelques concepts nouveaux dans l'analyse numérique de la chaetotaxie. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **15A**, 79–93.
- Nayrolles, P. (1993b). A standardised description of European Sminthuridae (Collembola, Symphypleona). 1. Genera *Lipothrix*, *Gisinurus* and *Caprainea*. *Bijdragen tot de Dierkunde*, **63**, 43–60.
- Nayrolles, P. (1993c). Contribution to the knowledge of European Bourletiellidae (Collembola, Symphypleona). 1. On a standard of description and on the genus *Fasciosminthurus* Gisin 1960 sensu Bretfeld 1992. *Revue Suisse de Zoologie*, **100**, 655–73.
- Nayrolles, P. (1994a). A standardised description of European Sminthuridae (Collembola, Symphypleona). 2. Review of four species of the genera *Allacma* and *Spatulosminthurus*. *Bijdragen tot de Dierkunde*, **64**, 151–62.
- Nayrolles, P. (1994b). La biométrie des caractères discontinus d'après le revêtement appendiculaire des Collemboles Symphypléones. II. Recherche de quelques variables chétotaxiques caractéristiques du quatrième segment antennaire. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **16A**, 437–52.
- Nayrolles, P. (1994c). Contribution to the knowledge of European Bourletiellidae (Collembola, Symphypleona). II. Redescription of three species and description of three new species of *Fasciosminthurus*. *Revue Suisse de Zoologie*, **101**, 315–33.
- Nayrolles, P. (1995a). Propositions pour un retour à la définition originelle de l'homologie, d'après l'analyse de la chétotaxie des collemboles. *Bulletin de la Société Zoologique de France*, **120**, 3–20.
- Nayrolles, P. (1995b). Taxonomy of European species of *Cassagnaudiella* and *Bourletiella* (Collembola, Symphypleona, Bourletiellidae). *Zoologica Scripta*, **24**, 43–60.
- Nayrolles, P. (1995c). A standardised description of European Sminthuridae (Collembola, Symphypleona). 3. Description of seven species of *Sminthurus*, including four new to science. *Bijdragen tot de Dierkunde*, **64**, 215–37.
- Nayrolles, P. and Betsch, J.M. (1993). Pour une théorie de la description chétotaxique chez les collemboles. *Annales de la Société Entomologique de France, N.S.*, **29**, 5–15.

- Nayrolles, P. and Lienhard, C. (1990). Description d'une nouvelles espèce de *Prorastriopes* de Suisse (Collembola, Symphypleona). *Revue Suisse de Zoologie*, **97**, 623–8.
- Newell, K. (1984a). Interaction between two decomposer basidiomycetes and Collembola under Sitka spruce: distribution, abundance and selective grazing. *Soil Biology and Biochemistry*, **16**, 227–34.
- Newell, K. (1984b). Interaction between two decomposer basidiomycetes and a collembolan under Sitka spruce: grazing and its potential effects on fungal distribution and litter decomposition. *Soil Biology and Biochemistry*, **16**, 235–9.
- Nicolet, H. (1847). Essai sur une classification des insectes aptères de l'ordre des Thysanures. *Annales de la Société Entomologique de France, Série 2*, **5**, 335–95.
- Nijjima, K. (1971). Seasonal changes in Collembola populations in a warm temperate forest of Japan. *Pedobiologia*, **11**, 11–26.
- Nijjima, K. (1973). Experimental studies on the life history, fecundity and growth of *Sinella curviseta* (Apterygota, Collembola). *Pedobiologia*, **13**, 186–204.
- Nijjima, K. (1975). Seasonal changes in collembolan populations in a warm temperate forest of Japan. II. Population dynamics of the dominant species. *Pedobiologia*, **15**, 40–52.
- Noble-Nesbitt, J. (1963a). Transpiration in *Podura aquatica* L. (Collembola Isotomidae) and the wetting properties of its cuticle. *Journal of Experimental Biology*, **40**, 681–700.
- Noble-Nesbitt, J. (1963b). A site of water and ionic exchange with the medium in *Podura aquatica* L. (Collembola, Isotomidae). *Journal of Experimental Biology*, **40**, 701–11.
- Noble-Nesbitt, J. (1963c). The fully formed intermoult cuticle and associated structures of *Podura aquatica* (Collembola). *Quarterly Journal of Microscopical Science*, **104**, 253–70.
- Noble-Nesbitt, J. (1963d). The cuticle and associated structures of *Podura aquatica* at the moult. *Quarterly Journal of Microscopical Science*, **104**, 369–91.
- Norton, R.A. and Ryabinin, N.A. (1994). New alpine damaeid mite (Acari, Oribatida) from New Hampshire, USA. *Acarologia*, **35**, 373–80.
- Nosek, J. (1981). Ecological niche of Collembola in biogeocoenoses. *Pedobiologia*, **21**, 166–71.
- Nosek, J. and Christian, E. (1983). *Onychiurus (Oligaphorura) pseudoraxensis* n.sp.: ein neuer Springschwanz (Hexapoda: Collembola) aus einer niederösterreichischen Höhle. *Annalen des Naturhistorischen Museums, Wien*, **84B**, 397–400.
- Nosek, J. and Paoletti, M.G. (1985). *Heteromurus (Verhoeffiella) dallaii* sp.n., a new cave-dwelling spring-tail (Collembola, Entomobryidae). *Revue Suisse de Zoologie*, **92**, 271–4.
- Nottrot, F., Joosse, E.N.G., and Van Straalen, N.M. (1987). Sublethal effects of iron and manganese soil pollution on *Orchesella cincta* (Collembola). *Pedobiologia*, **30**, 45–53.
- O'Hara, R.J. (1994). Evolutionary history and the species problem. *American Zoologist*, **34**, 12–22.
- Ohlsson, L. and Verhoef, H.A. (1988). Effects of diet composition on cold adaptation in temperate Collembola. *Comparative Biochemistry and Physiology*, **91A**, 475–9.
- Ojeda, M. and Palacios-Vargas, J.G. (1984). A new species of *Troglopedetes* (Collembola: Paronellidae) from Guerrero, Mexico. *Entomological News*, **95**, 23–6.
- Oken, L. (1833–1842). *Allgemeine Naturgeschichte für alle Stände*. Hoffman, Stuttgart.
- Oliveira, E. and Deharveng, L. (1990). *Isotomiella* (Collembola, Isotomidae) d'Amazonie: les espèces du groupe *minor*. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **12A**, 75–93.
- Oliveira, E. and Deharveng, L. (1994). Deux nouvelles espèces de *Pseudachorutes* d'Amazonie (Collembola, Neanuridae). *Bulletin de la Société Entomologique de France*, **99**, 389–95.
- Oliveira, E.P. and Franklin, E. (1993). The effect of fire on soil mesofauna: recolonization of burnt areas. *Pesquisa Agropecuaria Brasileira*, **28**, 357–69.
- Oliveira, E.P. and Thibaud, J.M. (1988). Un nouveau genre d'insecte Collembola Hypogastruridae d'Amazonie. *Amazoniana*, 299–302.
- Oliveira, E. and Thibaud, J.M. (1992). Notes sur les collembolés de l'Amazonie, Brésil. 1. Hypogastruridae et Onychiuridae, avec la description de deux espèces nouvelles (Collembola). *Opuscular Zoologica Fluminensis*, **95**, 1–8.
- Packard, A.S. (1888). The cave fauna of North America, with remarks on the anatomy of the brain and origin of the blind species. *Memoirs of the National Academy of Sciences*, **4**, 1–156.
- Pacit, J. (1956). *Biologie der primär flügellosen Insekten*. G. Fischer, Jena.
- Pacit, J. (1965). *Cyphoderus trinervoidis* n.sp., ein neuer Termitophile aus Trasvaal (Ins. Collembola). *Senckenbergiana biologica*, **46**, 59–60.
- Pacit, J. (1967). On South and Central African Collembola. *Journal of the Entomological Society of South Africa*, **29**, 135–47.
- Pacit, J. (1971). Zur Taxonomie hauptsächlich der schuppenlosen Entomobryinae. *Zoologischer Anzeiger*, **186**, 267–72.

- Palacios-Vargas, J.G. (1979). Nueva especie de *Schoettella* (Collembola: Hypogastruridae). *Folia Entomológica Mexicana*, **41**, 61–9.
- Palacios-Vargas, J.G. (1981). Collembola asociados a *Tillandsia* (Bromeliaceae) en el Derrame Lavico del Chichinutzin, Morelos, Mexico. *Southwestern Entomologist*, **6**, 87–98.
- Palacios-Vargas, J.G. (1983a). Collembolles cavernicoles du Mexique. *Pedobiologia*, **25**, 349–55.
- Palacios-Vargas, J.G. (1983b). Catalogo de los Collembola mexicanos. *An. Esc. nat. Cienc. biol., Mex.*, **27**, 61–76.
- Palacios-Vargas, J.G. (1984). Segunda especie mexicana de *Palmanura* Cassagnau and Palacios-Vargas (Collembola: Neanuridae). *Folia Entomológica Mexicana*, **59**, 3–10.
- Palacios-Vargas, J.G. (1986). Une nouvelle espèce de *Palmanura* et étude sur la chetotaxie de la lignée sensillanurienne (Collembola: Neanuridae). *Revue Française d'Entomologie*, N.S., **8**, 107–12.
- Palacios-Vargas, J.G. (1988). Collembolles Poduromorpha de Nouvelle-Calédonie. 4. *Friesea neocaledonica* n.sp. (Neanuridae, Frieseinae). *Mémoires du Muséum National d'Histoire Naturelle*, **142A**, 39–43.
- Palacios-Vargas, J.G. (1989). New records of cave Collembola from the Neotropical region and notes on their origin and distribution. *Proceedings of the 10th International Congress of Speleology*, **3**, 734–9.
- Palacios-Vargas, J.G. (1990a). Nuevos Collembola del Estado de Chihuahua, Mexico. *Folia Entomológica Mexicana*, **79**, 5–32.
- Palacios-Vargas, J.G. (1990b). Manuales y guías para el estudio de microartrópodos. I. Diagnósis y clave para determinar las familias de los Collembola de la región Neotropical. Programa: Ecología de Microartrópodos. Departamento de Biología, Facultad de Ciencias, Universidad Nacional Autónoma de México, pp. 1–15.
- Palacios-Vargas, J.G. (1991a). Manuales y guías para el estudio de microartrópodos. II. Introducción a los insectos sin alas. (Protura, Diplura, Collembola, Thysanura). Región Neotropical. Programa: Ecología de Microartrópodos. Departamento de Biología, Facultad de Ciencias, Universidad Nacional Autónoma de México, pp. 1–23.
- Palacios-Vargas, J.G. (1991b). XXI. Problemas en la taxonomía de algunos artrópodos: Hexapoda (Apterygota). In *Taxonomía biológica* (ed. J.L. Bousquets and I. Luna), pp. 397–418. Universidad Nacional Autónoma de México.
- Palacios-Vargas, J.G. (1992a). Nuevos datos sobre los colembolos y Acores cavernícolas en Argentina. *Spelaion (Buenos Aires)*, **3**, (3), 3–6.
- Palacios-Vargas, J.G. (1992b). Guide to the springtails of Panama and Costa Rica (Collembola). In *Insects of Panama and Mesoamerica. Selected studies* (ed. D. Quintero and A. Aiello), pp. 25–36. Oxford University Press.
- Palacios-Vargas, J.G. (1993). Evaluación de la fauna cavernícola terrestre de Yucatán, México. *Mémoires de Biospéologie*, **20**, 157–63.
- Palacios-Vargas, J.G. (1994). Biodiversidad de microartrópodos edáficos y cavernícolas de México. *Primeras Jornadas de Biología. Facultad de Ciencias Biológicas, Universidad de Guadalajara, México*, pp. 6–15.
- Palacios-Vargas, J.G. (1995). A new species of *Densiella* (Collembola: Sminthuridae) from Nicaragua. *Review of Nicaraguan Entomology*, **32**, 25–32.
- Palacios-Vargas, J.G. and Acosta, M.V.V. (1994). Nuevas especies de *Friesea* (Collembola: Neanuridae) de reservas biológicas de México. *Southwestern Entomologist*, **19**, 291–9.
- Palacios-Vargas, J.G. and Castillo, M.L. (1992). Sucesión ecológica de microartrópodos dentro de troncos en descomposición. *Boll. Soc. Mex. Entom.*, **11**, 23–30.
- Palacios-Vargas, J.G. and Deharveng, L. (1982). *Onychiurus acuitlapanensis* n.sp. (Collembola: Onychiuridae) cavernícola de México. *Nouvelle Revue d'Entomologie*, **12**, 3–7.
- Palacios-Vargas, J.G. and Deharveng, L. (1987). Quatre nouvelles espèces de Neanurinae (Collembola). *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **123**, 105–14.
- Palacios-Vargas, J.G. and Diaz, M. (1992). Dos nuevas especies de Neanuridos (Insecta: Collembola) de Cuba. *Caribbean Journal of Science*, **28**, 158–64.
- Palacios-Vargas, J.G. and Gnaspini-Netto, P. (1992). A new Brazilian species of *Acherontides* (Collembola: Hypogastruridae), with notes on its ecology. *Journal of the Kansas Entomological Society*, **65**, 443–7.
- Palacios-Vargas, J.G. and Gomez, J.A. (1991). Los colembolos y su relación con los hongos. XXVI Congreso Nacional de Entomología México. I. Simposio Nacional sobre la interacción Insecto-Hongo. Memorias, pp. 99–114.
- Palacios-Vargas, J.G. and Gomez-Anaya, J.A. (1993). Los Collembola (Hexapoda: Apterygota) de Chamela, Jalisco, México (distribución ecología y claves). *Folia Entomológica Mexicana*, **89**, 1–34.
- Palacios-Vargas, J.G. and Gomez-Anaya, J.A. (1995). Two new species of *Paleonura* (Collembola, Neanuridae). *Journal of the Kansas Entomological Society*, **68**, 95–102.

- Palacios-Vargas, J.G. and Gonzalez, V. (1995). Two new species of *Deuterosminthurus* (Bourletiellidae), epiphytic Collembola from the Neotropical region with a key for the American species. *Florida Entomologist*, **78**, 286–94.
- Palacios-Vargas, J.G. and Mejia, B.E. (1989). Colembolos de Jalisco, Mexico, con descripción de nuevas *Friezea* (Collembola: Neanuridae) y clave para determinar especies. *Folia Entomológica Mexicana*, **77**, 19–31.
- Palacios-Vargas, J.G. and Najt, J. (1981). Tres nuevas *Brachystomella* (Collembola: Neanuridae) de Mexico. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **117**, 263–71.
- Palacios-Vargas, J.G. and Najt, J. (1985). Trois nouveaux Odontellidae du Mexique (Collembola). *Revue Française d'Entomologie*, N.S., **7**, 89–95.
- Palacios-Vargas, J.G. and Najt, J. (1986). Collembola de las reservas de la biosfera Mexicana. I. Neanurinae. *Folia Entomológica Mexicana*, **68**, 5–27.
- Palacios-Vargas, J.G. and Vasquez, M.M. (1988). Three new species of littoral Collembola (Hypogastruridae) from Baja California Sur, Mexico. *Journal of the Kansas Entomological Society*, **61**, 433–40.
- Palacios-Vargas, J.G. and Wilson, J. (1990). *Troglobius coprophagus*, a new genus and species of cave Collembola from Madagascar, with notes on its ecology. *International Journal of Speleology*, **19**, 67–73.
- Palacios-Vargas, J.G., Ojeda, M., and Christiansen, K.A. (1985). Taxonomía y biogeografía de *Troglopedetes* (Collembola: Paronellidae) en América, con énfasis en las especies cavernícolas. *Folia Entomológica Mexicana*, **65**, 3–35.
- Palévody, C. (1965). Adaptation du Collembole troglophile *Folsomia candida* Willem var. *distincta* Bagnall aux conditions de vie de l'épéneuston. *Bulletin Scientifique de Bourgogne*, **23**, 153–93.
- Palévody, C. (1972). Microorganismes intracellulaires dans l'ovaire du Collembole Isotomidae *Folsomia candida*. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **175D**, 401–4.
- Palévody, C. (1976). *L'ovogenèse chez les Collemboles Isotomides: cytologie et approche physiologique*. PhD thesis, Université Paul Sabatier, Toulouse.
- Palévody, C. (1977). Perturbation du cycle reproducteur d'un Collembole par des microorganismes intracellulaires. *Revue d'Écologie et de Biologie du Sol*, **14**, 91–6.
- Palissa, A. (1964). Apterygota-Urinsekten. In *Die Tierwelt Mitteleuropas*, **4** (1a), *Insekten* (1), (ed. P. Brohmer, P. Ehrmann, and G. Ulmer), pp. 1–299. Quelle and Meyer, Leipzig.
- Palissa, A. (1986). *Onychiurus (Protaphorura) septempapillatus*, a new species of Collembola from the Salzgraben cave in the FRG. *Deutsche Entomologische Zeitschrift*, **33**, 227–31.
- Palissa, A. and Zivadinovic, J. (1974). Beiträge zur Collembolenfauna Jugoslawiens (I). *Deutsche Entomologische Zeitschrift*, **21**, 309–15.
- Park, O. (1949). A notable aggregation of Collembola. *Annals of the Entomological Society of America*, **42**, 7–9.
- Parkinson, D., Visser, S., and Whittaker, J.B. (1979). Effects of collembolan grazing on fungal colonization of leaf litter. *Soil Biology and Biochemistry*, **11**, 529–35.
- Parmalee, R.W., Wentzel, R.S., Phillips, C.T., Simini, M., and Checkai, R.T. (1993). Soil microcosm for testing the effects of chemical pollutants on soil fauna communities and trophic structure. *Environmental Toxicology and Chemistry*, **12**, 1477–86.
- Parr, T.W. (1978). An analysis of soil micro-arthropod succession. *Scientific Proceedings of the Royal Dublin Society*, **6A**, 185–96.
- Parsons, W.F.J. and Parkinson, D. (1986). Species composition, distribution and abundance of Collembola colonizing reclaimed mine spoil in Alberta. *Pedobiologia*, **29**, 33–45.
- Pass, G. (1991). Antennal circulatory organs in Onychophora, Myriapoda and Hexapoda: functional morphology and evolutionary implications. *Zoomorphology*, **110**, 145–64.
- Paulus, H.F. (1971). Einiges zur Cuticula-Struktur der Collembolen mit Bemerkungen zur Oberflächen-skulptur der Cornea. *Revue d'Écologie et de Biologie du Sol*, **8**, 37–44.
- Paulus, H.F. (1972). Zum Feinbau der Komplexaugen einiger Collembolen. Eine vergleichend-anatomische Untersuchung (Insecta, Apterygota). *Zoologische Jahrbücher für Anatomie*, **89**, 1–116.
- Paulus, H.F. (1974). Erster Nachweis von Scolopalorganen in den Gliederantennen eines entognathen Insekts (Collembola, Symphyleona). *Zeitschrift für Morphologie der Tiere*, **77**, 245–54.
- Pawert, M., Triebkorn, R., Graff, S., Berkus, M., Schulz, J., and Köhler, H.R. (1996). Cellular alterations in collembolan midgut cells as a marker of heavy metal exposure: ultrastructure and intracellular metal distribution. *Science of the Total Environment*, **181**, 187–200.
- Payne, J.A., King, E.W., and Beinhardt, G. (1968). Arthropod succession and decomposition of buried pigs. *Nature*, **219**, 1180–1.
- Peck, S. and Christiansen, K.A. (1990). Evolution and zoogeography of the invertebrate cave faunas of the driftless area of the Upper Mississippi Valley. *Canadian Journal of Zoology*, **68**, 73–88.

- Pedigo, L.P. (1967). Selected life history phenomena of *Lepidocyrtus cyaneus* f. *cinereus* Folsom with reference to grooming and the role of the collophore (Collembola: Entomobryidae). *Entomological News*, **78**, 263–7.
- Perfect, T.J., Cook, A.J., Critchley, B.R., and Russell-Smith, A. (1981). The effect of crop protection with DDT on the microarthropod population of a cultivated forest soil in the subhumid tropics. *Pedobiologia*, **21**, 7–18.
- Petersen, H. (1965). The Collembola of the Hansted Reserve, Thy, North Jutland. *Entomologiske Meddelelser*, **30**, 313–95.
- Petersen, H. (1971a). Collembolernes ernæringsbiologi og dennes økologiske betydning. *Entomologiske Meddelelser*, **39**, 97–118.
- Petersen, H. (1971b). Parthenogenesis in two common species of Collembola: *Tullerbergia krausbaueri* (Börner) and *Isotoma notabilis* Schäffer. *Revue d'Écologie et de Biologie du Sol*, **8**, 133–8.
- Petersen, H. (1971c). Methods for estimation of growth in Collembola in cultures and in the field, exemplified by preliminary results for *Onychiurus furcifer* (Börner). *Annales de Zoologie, Ecologie Animale*, **1971**, 235–54.
- Petersen, H. (1975). Estimation of dry weight, fresh weight, and calorific content of various Collembolan species. *Pedobiologia*, **15**, 222–43.
- Petersen, H. (1978). Sex ratios and the extent of parthenogenetic reproduction in some collembolan populations. In *First International Seminar on Apterygota* (ed. R. Dallai), pp. 19–35. Accademia delle Scienze di Siena detta de' Fisiocritici, Siena.
- Petersen, H. (1980). Population dynamics and metabolic characterization of Collembola species in a beech forest ecosystem. In *Soil biology as related to land use practices* (ed. D.L. Dindal), pp. 806–33. Environmental Protection Agency, Washington, D.C.
- Petersen, H. (1981). The respiratory metabolism of Collembola species from a Danish beechwood. *Oikos*, **37**, 273–86.
- Petersen, H. (1994). A review of collembolan ecology in ecosystem context. *Acta Zoologica Fennica*, **195**, 111–18.
- Petersen, H. (1995). Temporal and spatial dynamics of soil Collembola during secondary succession in Danish heathland. *Acta Zoologica Fennica*, **196**, 190–4.
- Petersen, H. and Luxton, M. (1982). A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, **39**, 287–388.
- Petersen, H., O'Neill, R.V., and Gardner, R.H. (1985). Use of an ecosystem model for testing ecosystem responses to inaccuracies of root and microflora productivity estimates. In *Ecological interactions in soil: plants, microbes and animals* (eds. A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher) pp. 233–42. Blackwell, Oxford.
- Peterson, A.J. (1971). Population studies on the antarctic Collembolan *Gomphiocephalus hodgsoni* (Carpenter). *Pacific Insects Monographs*, **25**, 75–98.
- Phillips, S.M. (1946). Occurrence of nematodes in a collembolan. *Entomologist's Monthly Magazine*, **82**, 218–19.
- Pichard, S. (1973). Contribution à l'étude de la biologie de *Podura aquatica* (Linné) Collembole. *Bulletin Biologique*, **108**, 191–9.
- Pichard, S., Massoud, Z., and Elkaim, B. (1989). Ecologie des peuplements de collembolles de quelques mares et de leurs abords en région parisienne. *Revue d'Écologie et de Biologie du Sol*, **26**, 451–72.
- Pike, E.M. (1994). Historical changes in insect community structure as indicated by hexapods of Upper Cretaceous Alberta (Grassy Lake) amber. *Canadian Entomologist*, **126**, 695–702.
- Pitkin, B.R. (1979). *Onychiurus arcticus* (Tullberg) (Collembola: Onychiuridae) an interesting new record to Britain, with a note on variation and distribution. *Revue d'Écologie et de Biologie du Sol*, **16**, 449–52.
- Pitkin, B.R. (1980). Variation in some British material of the *Onychiurus armatus* group (Collembola). *Systematic Entomology*, **5**, 405–26.
- Platnick, N.I. (1991). Patterns of diversity: tropical vs. temperate. *Journal of Natural History*, **25**, 1083–8.
- Poinar, G.O. (1992). *Life in amber*. Stanford University Press.
- Poinar, G.O. (1993). Insects in amber. *Annual Review of Entomology*, **46**, 145–59.
- Poinsot, N. (1966). Existence d'un comportement constructeur chez un Collembole, *Isotomidae Subisotoma variabilis* (Gisin, 1949). *Revue d'Écologie et de Biologie du Sol*, **3**, 173–8.
- Poinsot, N. (1970). Nouveaux exemples de comportement constructeur chez les Collembolles Isotomidae. *Revue du Comportement Animal*, **4**, 59–63.
- Poinsot, N. (1971). Ethologie de quelques espèces de Collembolles Isotomides de Provence. *Annales de l'Université de Provence, Sciences*, **45**, 33–53.
- Poinsot, N. (1972). Contribution à l'étude des Collembolles de Corse (Premiers note). *Nouvelle Revue d'Entomologie*, **2**, 293–8.

- Poinsot, N. and Dallai, R. (1970). Ricerche sui Collemboli. XIII. Contributo allo studio del genere *Proctostephanus*. *Redia*, **52**, 305–21.
- Poinsot-Balaguer, N. (1976). Contribution à l'étude de quelques espèces du groupe *Isotomurus palustris* (Müller) (Collembola, Isotomidae). *Annales de la Société Entomologique de France*, N.S., **12**, 639–52.
- Poinsot-Balaguer, N. (1988). Stratégies adaptives des arthropodes du sol en région méditerranéenne. In *Time scales and water stress* (ed. F. di Castri, C. Floret, S. Rambal, and J. Roy), pp. 511–39. IUBS, Paris.
- Poinsot-Balaguer, N. (1990). Des insectes résistants à la sécheresse. *Sécheresse*, **1**, 265–71.
- Poinsot-Balaguer, N. and Barra, J.A. (1977). Un nouveau type cellulaire dans le mésentéron de *Folsomia variabilis* (Collembola, Aptérygotes). *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **284D**, 45–7.
- Poinsot-Balaguer, N. and Barra, J.A. (1982). Révision systématique du genre *Folsomides* et apport de l'écophysiologie à la taxonomie de certaines espèces du genre (Insectes, Collembola). 2e note. *Revue d'Écologie et de Biologie du Sol*, **19**, 259–75.
- Poinsot-Balaguer, N. and Barra, J.A. (1983). Experimental and ultrastructural data on freezing resistance of *Folsomides angularis* (Insecta, Collembola). *Pedobiologia*, **25**, 357–63.
- Poinsot-Balaguer, N. and Barra, J.A. (1991). L'anhydrobiose: un problème biologique nouveau chez les collembola (Insecta). *Revue d'Écologie et de Biologie du Sol*, **28**, 197–205.
- Poinsot-Balaguer, N. and Tabone, E. (1995). Impact of chronic gamma irradiation on the litter decay of a mixed mediterranean forest in Cadarache, France. Microarthropod's response. *Pedobiologia*, **39**, 344–50.
- Poinsot-Balaguer, N., Castet, R., and Tabone, E. (1991). Impact of chronic gamma irradiation on a mediterranean forest ecosystem in Cadarache (France). *Journal of Environmental Radioactivity*, **14**, 23–36.
- Poinsot-Balaguer, N., Racon, L., Sadaka, N., and Lepetit, J. (1993). Effects of tannin compounds on two species of Collembola. *European Journal of Soil Biology*, **29**, 13–16.
- Pomorski, R.J. (1986). Morphological-systematic studies on the variability of pseudocellae and some morphological characters in 'armatus-group' (Collembola, Onychiuridae). Part I. *Onychiurus (Protaphorura) fimatus* Gisin 1952. *Polskie Pismo Entomologiczne*, **56**, 531–56.
- Pomorski, R.J. (1989). Notes on morphology and biology of a parthenogenetic population of *Onychiurus hortensis* Gisin, 1949 (Collembola, Onychiuridae). *Przegląd Zoologiczny*, **33**, 567–72.
- Pomorski, R.J. (1990a). *Onychiurus paxi* Stach, 1939, a junior synonym of *Onychiurus (Onychiurus) denisi* Stach, 1934 (Collembola). *Polskie Pismo Entomologiczne*, **60**, 59–63.
- Pomorski, R.J. (1990b). New data on the genus *Hymenaphorura* (Collembola, Onychiuridae) from Europe. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, **63**, 209–25.
- Pomorski, R.J. (1990c). Morphological-systematic studies on the variability of pseudocelli and some morphological characters in *Onychiurus* of the 'armatus-group' (Collembola, Onychiuridae). Part II. On synonyms within the 'armatus-group', with special reference to diagnostic characters. *Annales Zoologici (Warszawa)*, **43**, 535–76.
- Pomorski, R.J. (1992a). *Hymenaphorura hispanica* sp.n. of Collembola (Onychiuridae) from the Occidental Pyrenees. *Eos*, **68**, 3–5.
- Pomorski, R.J. (1992b). Collembola of caves and some adits of the Polish Sudetes. *Acta Universitatis Wratislaviensis*, **25**, 27–44.
- Pomorski, R.J. (1993). Two new species of *Protaphorura* Absolon, 1901, from North Karelia (Russia), with notes on the position of altered pseudocelli (psx) in the *armatus*-group (Collembola, Onychiuridae). *Genus (Wrocław)*, **4**, 121–8.
- Pomorski, R.J. (1994a). New data on epilittoral species of the genus *Anurida* Laboulbène, 1965 (Collembola, Neanuridae) in Poland. *Przegląd Zoologiczny*, **38**, 273–7.
- Pomorski, R.J. (1994b). *Protaphorura kopetdagi* n.sp. from Turkemia (Collembola: Onychiuridae). *Genus (Wrocław)*, **5**, 193–5.
- Pomorski, R.J. and Skarzynski, D. (1989). Notes on morphology of *Onychiurus (Onychiurus) rectopapillatus* Stach, 1933 (Collembola, Onychiuridae). *Polskie Pismo Entomologiczne*, **59**, 305–9.
- Pomorski, R.J. and Skarzynski, D. (1992). *Collembola Polski*. Biologica Silesiae, Warsaw.
- Pomorski, R.J. and Skarzynski, D. (1994). A redescription of *Anurida elipsoides* Stach, 1949 (Collembola: Neanuridae). *Genus (Wrocław)*, **5**, 367–70.
- Pomorski, R.J. and Weichsel, M. (1993). Building behaviour in *Hymenaphorura polonica* Pomorski, 1990 (Collembola, Onychiuridae). *Polskie Pismo Entomologiczne*, **62**, 273–6.
- Ponge, J.F. (1983). Les collembola, indicateurs du type d'humus en milieu forestier. Resultats obtenus au Sud de Paris. *Acta Oecologia, Oecologia Generalis*, **4**, 359–74.
- Ponge, J.F. (1991a). Food resources and diets of soil animals in a small area of Scots pine litter. *Geoderma*, **49**, 33–62.

- Ponge, J.F. (1991b). Succession of fungi and fauna during decomposition of needles in a small area of Scots pine litter. *Plant and Soil*, **138**, 99–113.
- Ponge, J.F. (1993). Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems. *Pedobiologia*, **37**, 223–44.
- Ponge, J.F. and Charpentié, M.J. (1981). Étude des relations microflore-microfaune: expériences sur *Pseudosinella alba* (Packard), collembole mycophage. *Revue d'Écologie et de Biologie du Sol*, **18**, 291–303.
- Ponge, J.F. and Prat, B. (1982). Les Collembolés, indicateurs du mode d'humification dans les peuplements résineux, feuillus et mélangés: résultats obtenus en forêt d'Orléans. *Revue d'Écologie et de Biologie du Sol*, **19**, 237–50.
- Ponge, J.F., Arpin, P., and Vannier, G. (1993). Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem. *European Journal of Soil Biology*, **29**, 141–53.
- Poole, T.B. (1959). Studies on the food of Collembola in a Douglas fir plantation. *Proceedings of the Zoological Society of London*, **132**, 71–82.
- Poole, T.B. (1961). An ecological study of the Collembola in a coniferous forest soil. *Pedobiologia*, **1**, 113–37.
- Poole, T.B. (1962). The effect of some environmental factors on the pattern of distribution of soil Collembola in a coniferous woodland. *Pedobiologia*, **2**, 169–82.
- Poole, T.B. (1964). A study of the distribution of soil Collembola in three small areas in a coniferous woodland. *Pedobiologia*, **4**, 35–42.
- Popovici, I., Stan, G., Stefan, V., Tomescu, R., Dumea, A., Tarta, A., and Dan, F. (1977). The influence of atrazine on soil fauna. *Pedobiologia*, **17**, 209–15.
- Posthuma, L. (1990). Genetic differentiation between populations of *Orchesella cincta* (Collembola) from heavy metal contaminated sites. *Journal of Applied Ecology*, **27**, 609–22.
- Posthuma, L. and Janssen, G.M. (1995). Genetic variation for life history characteristics in reference populations of *Orchesella cincta* (L.) in relation to evolutionary responses to metals in soils. *Acta Zoologica Fennica*, **196**, 301–6.
- Posthuma, L. and Van Straalen, N.M. (1993). Heavy-metal adaptation in terrestrial invertebrates: a review of occurrence, genetics, physiology and ecological consequences. *Comparative Biochemistry and Physiology*, **106C**, 11–38.
- Posthuma, L., Hogervorst, R.F., and Van Straalen, N.M. (1992). Adaptation to soil pollution by cadmium excretion in natural populations of *Orchesella cincta* (L.) (Collembola). *Archives of Environmental Contamination and Toxicology*, **22**, 146–56.
- Posthuma, L., Hogervorst, R.F., Joosse, E.N.G., and Van Straalen, N.M. (1993a). Genetic variation and covariation for characteristics associated with cadmium tolerance in natural populations of the springtail *Orchesella cincta* (L.). *Evolution*, **47**, 619–31.
- Posthuma, L., Verweij, R.A., Widianarko, B., and Zonneveld, C. (1993b). Life-history patterns in metal-adapted Collembola. *Oikos*, **67**, 235–49.
- Potapov, M.B. (1988). Description of a new genus of Isotomidae (Collembola) from mountain regions of the USSR. *Zoologicheskij Zhurnal*, **67**, 144–8.
- Potapov, M. (1989). The use of sensorial chaetotaxy in taxonomy of some Isotomidae (Collembola). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 35–42. University of Siena, Siena.
- Potapov, M. (1991a). *Antarctophorus*: a new genus of Isotomidae (Collembola) from Antarctica. *Revue d'Écologie et de Biologie du Sol*, **28**, 491–5.
- Potapov, M.B. (1991b). Species of the genus *Isotoma* subgenus *Parisotoma* Bagnall 1940 and *Sericeotoma* subgen. nov. (Collembola, Isotomidae) of USSR fauna. *Acta Zoologica Cracoviensia*, **34**, 267–301.
- Potapov, M.B. and Banasko, J.A. (1985). A new species of springtail from Cuba with comments on the role of chaetotaxy in diagnostics of the *Friezea* (Collembola, Neanuridae) species. *Zoologicheskij Zhurnal*, **64**, 1162–7.
- Potapov, M.B. and Karpus, I.J. (1993). Species of the genus *Tetracanthella* (Collembola, Isotomidae) from the Ukrainian Carpathian. *Zoologicheskij Zhurnal*, **72**, 30–5.
- Potapov, M.B. and Kuchiev, I.T. (1993). Species of the genus *Tetracanthella* (Collembola, Isotomidae) from the Crimea and the Caucasus. *Zoologicheskij Zhurnal*, **72**, 36–43.
- Potapov, M.B. and Stebaeva, S. (1992). Redescription and systematic position of *Heteroisotoma* Stach (Collembola: Isotomidae). *Entomologica Scandinavica*, **22**, 427–31.
- Potapov, M.B. and Stebaeva, S. (1994). *Sibiracanthella* and *Sahacanthella* new genera of Anurophorinae (Collembola, Isotomidae) with anal spines from continental Asia. *Miscellaneous Zoology*, **17**, 129–39.
- Poursin, J.M. and Ponge, J.F. (1984). Étude des peuplements de microarthropodes (Insectes Collembola et Acariens Oribates) dans trois humus forestiers acides de la forêt d'Orléans (Loiret, France). *Pedobiologia*, **26**, 403–14.

- Pouyat, R.V., Parmelee, R.W., and Carreiro, M.M. (1994). Environmental effects of forest soil-invertebrate and fungal densities in oak stands along an urban-rural land use gradient. *Pedobiologia*, **38**, 385–99.
- Pozo, J. (1986). Ecological factors affecting Collembola populations. Ordination of communities. *Revue d'Écologie et de Biologie du Sol*, **23**, 299–311.
- Pozo, J., Selga, D., and Simon, J.C. (1986). Studies of the collembolan populations of several plant communities of the Basque Country (Spain). *Revue d'Écologie et de Biologie du Sol*, **23**, 215–32.
- Prabhoo, N.R. (1971a). Soil and litter Collembola of South India. I. Arthropleona. *Oriental Insects*, **5**, 1–46.
- Prabhoo, N.R. (1971b). Bark and moss inhabiting Collembola of South India. *Bulletin of Entomology*, **12**, 41–7.
- Prabhoo, N.R. (1986). Collembolan community in a bamboo grove and grass plot. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 149–55. University of Siena, Siena.
- Prabhoo, N.R. (1987). Recent trends in the biosystematics of entognathous apterygota with special reference to Collembola. *Proceedings of the Indian Academy of Sciences, Animal Sciences*, **96**, 619–28.
- Prabhoo, N.R. and Pai, C.G.A. (1986). Collembola of fire affected and control sites in the Ponmudi-Kallar region of the Western Ghats in India. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 157–62. University of Siena, Siena.
- Prat, B. and Massoud, Z. (1980). Étude de la communauté des Collembolles dans un sol forestier. I. Structure du peuplement. *Revue d'Écologie et de Biologie du Sol*, **17**, 199–216.
- Prat, B. and Massoud, Z. (1981). Étude de la communauté des Collembolles dans un sol forestier. II. Evolution du peuplement. *Revue d'Écologie et de Biologie du Sol*, **18**, 59–76.
- Prat, B. and Massoud, Z. (1982). Étude de la communauté des Collembolles dans un sol forestier. III. Phénologie des espèces. *Revue d'Écologie et de Biologie du Sol*, **19**, 403–10.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., and Gibbons, D.W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335–7.
- Price, P.W. (1988). An overview of organismal interactions in ecosystems in evolutionary and ecological time. *Agriculture, Ecosystems and Environment*, **24**, 369–77.
- Pritchard, G., McKee, M.H., Pike, E.M., Scrimgeour, G.J., and Zloty, J. (1993). Did the first insects live in water or air? *Biological Journal of the Linnean Society*, **49**, 31–44.
- Purrington, F.F., Kendall, P.A., Bater, J.E., and Stinner, B.R. (1991). Alarm pheromone in a gregarious Poduromorph Collembolan (Collembola, Hypogastruridae). *Great Lakes Entomologist*, **24**, 75–8.
- Purrini, K. (1982). Light and electron microscopic studies on three microsporidians (Microsporidia, Microspora) parasitizing springtails (Collembola, Apterygota). *Archiv für Protistenkunde*, **126**, 383–92.
- Purrini, K. (1983). Comparison of pathogenic agents in Collembola (Insecta, Apterygota) from different forests in the Federal Republic of Germany, Austria and Spain. *Pedobiologia*, **25**, 365–71.
- Purrini, K. (1984a). Light and electron microscope studies on *Helicosporidium* sp. parasitizing oribatid mites (Oribatei, Acarina) and Collembola (Apterygota, Insecta) in forest soils. *Journal of Invertebrate Pathology*, **44**, 18–27.
- Purrini, K. (1984b). Two new coccidian parasites of the genus *Adelina* (Adeleidae, Coccidia) parasitizing oribatid mite *Nothrus silvestris* (Oribatei, Acarina) and springtail *Neanura muscorum* (Collembola, Apterygota) in forest soils. *Archiv für Protistenkunde*, **128**, 99–107.
- Purvis, G. and Curry, J.P. (1980). Successional changes in the arthropod fauna of a new ley pasture established on previously cultivated arable land. *Journal of Applied Ecology*, **17**, 309–21.
- Queiroz, K. de and Gauthier, J. (1994). Towards a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution*, **9**, 27–31.
- Quicke, D.L.J. (1993). *Principles and techniques of contemporary taxonomy*. Blackie, Glasgow.
- Rabitsch, W.B. (1995). Metal accumulation in arthropods near a lead/zinc smelter in Arnoldstein, Austria. I. *Environmental Pollution*, **90**, 221–37.
- Rand, D.A. and Wilson, H.B. (1993). Evolutionary catastrophes, punctuated equilibria and gradualism in ecosystem evolution. *Proceedings of the Royal Society of London*, **253B**, 137–41.
- Rapoport, E.H. (1962a). Colémbolos de Bahía Blanca (Argentina). III. *Publicaciones del Instituto de Edafología e Hidrología*, **2**, 1–24.
- Rapoport, E.H. (1962b). Colémbolos de Bahía Blanca (Argentina). IV. *Acta Zoologica Lilloana*, **18**, 443–55.
- Rapoport, E.H. (1962c). Un caso teratológico en *Hypogastrura viatica* (Tullberg) (Collembola: Hypogastruridae). *Physis*, **23**, 272.
- Rapoport, E.H. (1969a). Gloger's rule and pigmentation of Collembola. *Evolution*, **23**, 622–6.
- Rapoport, E.H. (1969b). Collembola of Tristan da Cunha, Nightingale and Inaccessible Islands. *Nytt Magasin for Zoologi*, **18**, 23–32.
- Rapoport, E.H. (1971). The geographical distribution of Neotropical and Antarctic Collembola. *Pacific Insects Monographs*, **25**, 99–118.

- Rapoport, E.H. and Aguirre, Y. (1973). Population analysis of *Onychiurus yolandae*, a parthenogenetic collembolan insect with notes on possible prey tactics. *Revue d'Écologie et de Biologie du Sol*, **10**, 341–58.
- Raynal, G. (1974). Influence de l'humidité du substrat sur l'apparition de la neutralisation phénotypique chez *Bourletiella radula* (Collembola, Sminthuridae). *Pedobiologia*, **14**, 182–90.
- Raynal, G. (1976). Les populations de *Bourletiella radula* G. (Coll. Sminthuridae) du Plateau d'Aumar (Hautes Pyrénées). Conditions d'apparition des formes neutralisées. *Bulletin de la Société d'Histoire Naturelle de Toulouse*, **112**, 23–35.
- Reddy, M.V. (1983). The effect of controlled burning on the edaphic microarthropod population densities in a pine, *Pinus kesiya* Royle plantation. *Journal of Environmental Biology*, **4**, 149–53.
- Reddy, M.V. (1986). Soil-inhabiting arthropods as indicators of environmental quality. *Acta Biologica Hungarica*, **37**, 79–84.
- Reddy, M.V. (1992). Effects of microarthropod abundance and abiotic variables on mass-loss, and concentrations of nutrients during decomposition of *Azadirachta indica* leaf litter. *Tropical Ecology*, **33**, 89–96.
- Reddy, M.V. and Alfred, J.R.B. (1989a). Some abiotic factors affecting seasonal changes in soil arthropod populations in a pine ecosystem. *Journal of Ecobiology*, **1**, 24–33.
- Reddy, M.V. and Alfred, J.R.B. (1989b). Seasonal abundance of microarthropods of needle litter during decomposition in a pine plantation in relation to litter mass-loss, moisture and temperature. *Journal of Soil Biology and Ecology*, **9**, 104–17.
- Reddy, M.V. and Toky, O.P. (1990). Decomposition of grass, bamboo and tree litter in relation to microarthropod densities and abiotic factors in a 'Jhum' fallow of northeast India. *Journal of Soil Biology and Ecology*, **10**, 27–35.
- Reddy, M.V. and Venkataiah, B. (1986). Responses of soil-surface inhabiting arthropods following harvesting cane in a sugarcane agroecosystem. *Acta Ecologia (India)*, **8**, 20–3.
- Reddy, M.V. and Venkataiah, B. (1990a). Seasonal abundance of soil-surface arthropods in relation to some meteorological and edaphic variables of the grassland and tree-planted areas in a tropical semi-arid savanna. *International Journal of Biometeorology*, **34**, 49–59.
- Reddy, M.V. and Venkataiah, B. (1990b). Effects of tree plantation on qualitative and quantitative composition of soil arthropods of a semi-arid tropical savanna. *Environment and Ecology*, **8**, 361–7.
- Reddy, M.V. and Venkataiah, B. (1990c). Effects of tree plantation on seasonal community structure of soil microarthropods in a tropical semi-arid savanna. *Tropical Ecology*, **31**, 96–105.
- Reichle, D.E. and Crossley, D.A. (1965). Radiocesium dispersion in a cryptozoan food web. *Health Physics*, **11**, 1375–84.
- Reuter, L. and Reuter, O.M. (1880). Collembola and Thysanura found in Scotland in the Summer of 1876. *Scottish Naturalist*, **5**, 204–8.
- Reuter, O.M. (1895). Apterygogenea fennica. *Acta Societatis pro Fauna et Flora Fennica*, **11**, (4), 1–35.
- Rice, W.R. and Hostert, E.E. (1993). Laboratory experiments on speciation: what have we learned in 40 years? *Evolution*, **47**, 1637–53.
- Richard, K.J., Convey, P., and Block, W. (1994). The terrestrial arthropod fauna of the Byers Peninsula, Livingstone Island, South Shetland Islands. *Polar Biology*, **14**, 371–9.
- Richards, W.R. (1968). Generic classification, evolution and biogeography of the Sminthuridae of the World (Collembola). *Memoirs of the Entomological Society of Canada*, **53**, 1–54.
- Richards, W.R. (1979). Collembola. *Memoirs of the Entomological Society of Canada*, **108**, 300–3.
- Rickerl, D.H. (1986). Levels of *Rhizoctonia* and Collembola as affected by tillage and cropping system. *Phytopathology*, **76**, 1120.
- Rickerl, D.H., Curl, E.A., and Touchton, J.T. (1989). Tillage and rotation effects on Collembola populations and *Rhizoctonia* infestation. *Soil and Tillage Research*, **15**, 41–9.
- Ridley, H.N. (1880). A new species of *Lipura*. *Entomologist's Monthly Magazine*, **17**, 1–2.
- Roback, S.S. (1981). Collembola described by Scott, H.G. in the collections of the Academy of Sciences of Philadelphia. *Entomological News*, **92**, 209–10.
- Rosciszewska, E. (1985). Ultrastructure of surface cuticle of *Tetrodontophora bielanensis* (Waga) (Collembola). *Acta Biologica Cracoviensis, Zoologie*, **27**, 39.
- Rosciszewska, E. and Ksiazkiewicz, M. (1981). Ultrastructure of the transporting epithelium of tubus ventralis in *Tetrodontophora bielanensis* (Waga) (Collembola). *Cytobios*, **31**, 151–62.
- Rosgen, C., Gerdsmeyer, J., and Greven, H. (1993). Die Wirkung zweier Streusalze auf Collembolengemeinschaften eines Wiesenbodens. *Pedobiologia*, **37**, 107–20.
- Röske, H. (1989). Collembola fauna on different types of agriculturally used soil. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 283–90. University of Siena, Siena.
- Roth, M. (1993). Investigations on lead in the soil invertebrates of a forest ecosystem. *Pedobiologia*, **37**, 270–9.
- Rothery, P. and Block, W. (1992). Characterizing supercooling point distributions. *Cryo Letters*, **13**, 193–8.

- Ruhfus, B. and Zinkler, D. (1995). Investigations on the sources utilized for the energy supply fuelling the jump of springtails. *Journal of Insect Physiology*, **41**, 297–301.
- Rusek, J. (1971). Zweiter Beitrag zur Kenntnis der Collembola (Apterygota) Chinas. *Acta Entomologica Bohemoslovaca*, **68**, 108–37.
- Rusek, J. (1974a). Die Präparation von Kleininsekten. *Mikrokosmos*, **63**, 10–12.
- Rusek, J. (1974b). Zur Taxonomie der Tullbergiinae (Apterygota: Collembola). *Vestník Československé Společnosti Zoologické*, **38**, 61–70.
- Rusek, J. (1975a). Die bodenbildende Funktion von Collembolen und Acarina. *Pedobiologia*, **15**, 299–308.
- Rusek, J. (1975b). Eine Präparationstechnik für Springschwänze und ähnliche Gliederfüßer. *Mikrokosmos*, **65**, 378–81.
- Rusek, J. (1975c). Zwei neue Tullbergiinae-Gattungen (Apterygota: Collembola). *Vestník Československé Společnosti Zoologické*, **39**, 231–40.
- Rusek, J. (1976). New Onychiuridae (Collembola) from Vancouver Island. *Canadian Journal of Zoology*, **54**, 19–41.
- Rusek, J. (1977). The status of *Tomolonus* Mills, 1948 (Collembola: Tomoceridae). *Revue d'Écologie et de Biologie du Sol*, **14**, 225–30.
- Rusek, J. (1978a). Wir züchten Springschwänze. *Mikrokosmos*, **68**, 52–5.
- Rusek, J. (1978b). New Palearctic taxa of Tullbergiinae (Collembola). *Acta Entomologica Bohemoslovaca*, **75**, 255–71.
- Rusek, J. (1979a). Ecological specialisation in some *Mesaphorura* species (Collembola, Tullbergiinae). *Acta Entomologica Bohemoslovaca*, **76**, 1–9.
- Rusek, J. (1979b). New Palearctic Anurophorinae (Collembola). *Vestník Československé Společnosti Zoologické*, **43**, 138–42.
- Rusek, J. (1980a). Notes on three *Folsomia* species (Collembola). *Vestník Československé Společnosti Zoologické*, **44**, 139–45.
- Rusek, J. (1980b). Morphology of juvenile instars in two *Mesaphorura* species (Collembola: Tullbergiinae). *Revue d'Écologie et de Biologie du Sol*, **17**, 583–9.
- Rusek, J. (1981). Some Collembola from Irak. *Vestník Československé Společnosti Zoologické*, **45**, 63–80.
- Rusek, J. (1982a). European *Mesaphorura* species of the *sylvatica*-group (Collembola, Onychiuridae, Tullbergiinae). *Acta Entomologica Bohemoslovaca*, **79**, 14–30.
- Rusek, J. (1982b). *Multivesicula* gen.n. from the subfamily Tullbergiinae (Collembola: Onychiuridae). *Vestník Československé Společnosti Zoologické*, **46**, 33–44.
- Rusek, J. (1984a). A new location and type of pseudocelli in *Onychiurus* spp. (Collembola, Onychiuridae). *Annales de la Société Royale Zoologique de Belgique*, **114**, 3–7.
- Rusek, J. (1984b). New species and review of the *Isotoma notabilis* species group (Collembola, Isotomidae). *Acta Entomologica Bohemoslovaca*, **81**, 343–69.
- Rusek, J. (1985a). Soil microstructures—contributions on specific soil organisms. *Quaestiones Entomologicae*, **21**, 497–514.
- Rusek, J. (1985b). *Blissia glabra* gen.n., sp.n. (Collembola: Isotomidae) from northwestern Canada. *Canadian Journal of Zoology*, **63**, 2077–82.
- Rusek, J. (1985c). *Lanzhotia brachycera* gen.n., sp.n. from central Europe (Collembola, Pseudachorutidae). *Acta Entomologica Bohemoslovaca*, **82**, 175–9.
- Rusek, J. (1985d). New Palearctic *Lepidocyrtus* and *Pseudosinella* species (Collembola: Entomobryidae). *Vestník Československé Společnosti Zoologické*, **49**, 132–46.
- Rusek, J. (1986a). European species of *Mesaphorura* and related genera (Collembola: Onychiuridae). In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 73–8. University of Siena, Siena.
- Rusek, J. (1986b). Notes on Collembolan chaetotaxy. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 79–83. University of Siena, Siena.
- Rusek, J. (1987a). Protection of soil organisms and improvement of biological properties of soil. In *Agricultural development and environmental research: American and Czechoslovak perspectives* (ed. A.S. Phillips and G.E. Schweitzer), pp. 89–96. Czechoslovak Academy of Sciences and U.S. National Academy of Sciences.
- Rusek, J. (1987b). New types of linea ventralis in Collembola and its function. In *Soil fauna and soil fertility* (ed. B.R. Striganova), pp. 699–706. Nauka, Moscow.
- Rusek, J. (1989a). Ecology of Collembola. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 271–81. University of Siena, Siena.
- Rusek, J. (1989b). Collembola and Protura in a meadow-forest ecotone. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 413–18. University of Siena, Siena.

- Rusek, J. (1990). Collembola and other microarthropods. In *Succession in abandoned fields: studies in Central Bohemia, Czechoslovakia* (ed. J. Osbornova, M. Kovarova, J. Leps, and K. Prach), pp. 55–8. Kluwer, Dordrecht.
- Rusek, J. (1991a). New Holarctic and Palearctic taxa of Tullbergiinae (Collembola). *Acta Entomologica Bohemoslovaca*, **55**, 65–75.
- Rusek, J. (1991b). Three new species of Pseudachorutini (Collembola: Neanuridae). *Acta Societatis Zoologicae Bohemoslovenicae*, **55**, 120–9.
- Rusek, J. (1991c). *Odontella delamarei* sp.n. from Central Europe (Collembola, Odontellidae). *Revue d'Écologie et de Biologie du Sol*, **28**, 113–17.
- Rusek, J. (1991d). *Sibirisotoma stebajevae* gen.n. sp.n. from Siberia (Collembola, Isotomidae). *Acta Entomologica Bohemoslovaca*, **88**, 33–7.
- Rusek, J. (1991e). New tropical Tullbergiinae (Collembola, Onychiuridae). *Acta Entomologica Bohemoslovaca*, **88**, 145–55.
- Rusek, J. (1991f). Some soil biological aspects of low-energy agriculture. In *International workshop on low energy agriculture* (ed. T. Vasko), pp. 85–91. South Bohemian Biological Centre, České Budejovice.
- Rusek, J. (1992). Distribution and dynamics of soil organisms across ecotones. In *Landscape boundaries: consequences for biotic diversity and ecological flows* (ed. A.J. Hansen and F. di Castri), pp. 196–214. Springer Verlag, New York.
- Rusek, J. (1993). Air-pollution-mediated changes in alpine ecosystems and ecotones. *Ecological Applications*, **3**, 409–16.
- Rusek, J. (1994). Succession of Collembola and some ecosystem components on a pingo in the Mackenzie River Delta, N.W.T., Canada. *Acta Zoologica Fennica*, **195**, 119–23.
- Rusek, J. and Marshall, V.G. (1976). *Tetracanthella pacifica* sp.n. (Collembola; Isotomidae) from British Columbia). *Canadian Entomologist*, **108**, 759–65.
- Rusek, J. and Weyda, F. (1981). Morphology, ultrastructure and function of pseudocelli in *Onychiurus armatus* (Collembola, Onychiuridae). *Revue d'Écologie et de Biologie du Sol*, **18**, 127–33.
- Rusek, J., Ulehlova, B., and Unar, J. (1975). Soil biological features of some alpine grasslands in Czechoslovakia. In *Progress in soil zoology* (ed. J. Vanek), pp. 199–215. Academia, Prague.
- Sadaka, N. and Poinso-Balaguer, N. (1987). Relations trophiques entre le collembole *Onychiurus zschokkei* Handschin et des feuilles de chêne vert *Quercus ilex* (L.), à divers stades de décomposition. *Revue d'Écologie et de Biologie du Sol*, **24**, 329–40.
- Sadaka, N. and Poinso-Balaguer, N. (1989). Relations trophiques feuilles de chêne vert (*Quercus ilex* L.): Collembolles. Influence de la qualité du matériel foliaire sur la croissance ponérale d'*Onychiurus zschokkei* Handschin. *Revue d'Écologie et de Biologie du Sol*, **26**, 197–204.
- Sadaka, N., Poinso-Balaguer, N., and Talin, J. (1989). Relations trophique feuilles de chêne vert (*Q. ilex* L.): Collembolles. Influence de la qualité du matériel foliaire sur la biologie d'*Onychiurus zschokkei* Handschin et *Folsomia candida* Willem. *Vie et Milieu*, **39**, 33–9.
- Saitoh, K. and Chiba, S. (1959). Notes on the chromosomes of a springtail *Tomocerus minutus* Tullberg (Collembola, Insecta). *Japanese Journal of Genetics*, **34**, 105–6.
- Salmon, J.T. (1941). The Collembolan fauna of New Zealand, including a discussion of its distribution and affinities. *Transactions of the Royal Society of New Zealand*, **70**, 282–431.
- Salmon, J.T. (1959). Concerning the Collembola Onychiuridae. *Transactions of the Royal Entomological Society of London*, **111**, 119–56.
- Salmon, J.T. (1962a). New Collembola from 83 deg. South in Antarctica. *Transactions of the Royal Society of New Zealand (Zoology)*, **2**, 147–52.
- Salmon, J.T. (1962b). A new species and redescrptions of Collembola from Antarctica. *Pacific Insects*, **4**, 887–94.
- Salmon, J.T. (1964). An index to the Collembola. *Royal Society of New Zealand Bulletin*, **7**, 1–651.
- Salmon, J.T. (1965a). Two new genera of Antarctic Collembola. *Pacific Insects*, **7**, 468–72.
- Salmon, J.T. (1965b). New Onychiurid Collembola from India and New Guinea. *Transactions of the Royal Society of New Zealand (Zoology)*, **5**, 225–31.
- Salmon, J.T. (1969). New Collembola from India. *Zoological Publications from the Victoria University of Wellington*, **51**, 40–9.
- Salmon, J.T. (1970a). Apterygota. *New Zealand Entomologist*, **4**, 30–2.
- Salmon, J.T. (1970b). Some new records and new species of Collembola from India. *Transactions of the Royal Society of New Zealand*, **12**, 145–52.
- Salmon, J.T. (1974a). Notes and drawings from type material of Collembola. *Zoological Publications from the Victoria University of Wellington*, **66**, 1–41.

- Salmon, J.T. (1974b). Concerning the Collembola Tullbergiinae. *Zoological Publications from the Victoria University of Wellington*, **67**, 1–19.
- Samways, M.J. (1994). *Insect conservation biology*. Chapman and Hall, London.
- Sankey, J.H.P. (1952). Swarming of *Achorutes longispinus* Tullb. *Entomologist's Monthly Magazine*, **88**, 92.
- Santos, F.P. and Whitford, W.G. (1981). The effects of microarthropods on litter decomposition in a Chihuahuan desert ecosystem. *Ecology*, **62**, 654–63.
- Sartori, M. (1991). Liste des types deposees au Musée de Zoologie, Lausanne. 2. Collembola, Odonata, Psocoptera, Neuroptera, Strepsiptera (Insecta). *Bulletin de la Société Vaudoise des Sciences Naturelles*, **80**, 357–60.
- Saur, E. and Ponge, J.F. (1988). Alimentary studies on the collembolan *Paratullbergia callipygos* using transmission electron microscopy. *Pedobiologia*, **31**, 355–79.
- Schaefer, M. and Schauer mann, J. (1990). The soil fauna of beech forests: comparison between a mull and a moder soil. *Pedobiologia*, **34**, 299–314.
- Schaeffer, J.C. (1766). *Elementa entomologica. Einleitung in die insectenkenntnis*. Gedruckt mit Weissischen Schriften, Regensburg.
- Schäffer, C. (1897). Apterygoten. *Hamburger Magalhaensische Sammelreise, Apterygoten*, pp. 1–48.
- Schaller, F. (1970). Collembola (springschwänze). In *Handbuch der Zoologie*, Vol. 4 (2) (ed. W. Kükenthal), pp. 1–72. Walter de Gruyter, Berlin.
- Schaller, F. (1992). *Isotoma saltans* und *Cryptopygus antarcticus*, Lebenskünstler unter Extrembedingungen (Collembola: Isotomidae). *Entomologia Generalis*, **17**, 161–7.
- Schaller, F. and Kopeszki, H. (1991). Zur Biologie von *Cryptopygus antarcticus* (Willem 1902) (Collembola: Isotomidae), mit kurzen Hinweisen auf den besonderen karyologischen Status der Art. *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, **198**, 217–28.
- Schenker, R. (1983). Effects of temperature acclimation on cold-hardiness of alpine micro-arthropods. *Revue d'Écologie et de Biologie du Sol*, **20**, 37–47.
- Schenker, R. (1984). Effects of temperature acclimation on cold-hardiness of Antarctic micro-arthropods. *Revue d'Écologie et de Biologie du Sol*, **21**, 205–20.
- Schenker, R. and Block, W. (1986). Microarthropod activity in three contrasting terrestrial habitats on Signy Island, maritime Antarctic. *British Antarctic Survey Bulletin*, **71**, 31–43.
- Schlegel, D. and Bauer, T. (1994). Capture of prey by two pseudoscorpion species. *Pedobiologia*, **38**, 361–73.
- Schliwa, W. (1965). Vergleichend anatomisch-histologische Untersuchungen über die Spermatophorenbildung bei Collembolen. *Zoologische Jahrbücher für Anatomie*, **82**, 445–520.
- Scholle, G., Wolters, V., and Schaefer, M. (1995). Mesofauna reaction to microbial growth conditions during the early stage of leaf litter decomposition. *Acta Zoologica Fennica*, **196**, 171–5.
- Schött, H. (1893a). Zur Systematik und Verbreitung palaearktischer Collembolen. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **25**, (2), 1–100.
- Schött, H. (1893b). Zwei neue Collembola aus dem Indischen Archipel. *Entomologisk Tidskrift*, **1893**, 171–6.
- Schreiber, R.F. and Eisenbeis, G. (1985). The uptake of organic molecules by the ventral tube of *Tomocerus flavescens* (Tullberg 1871) (Insecta, Collembola). *Journal of Insect Physiology*, **31**, 59–70.
- Schultz, H.J. (1991). Further contribution to the Collembola fauna of the Hiddensee Island (Insecta, Collembola). *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **65**, (7), 3–9.
- Schultz, H.J. (1994). Cave Collembola from the Harz and Kyffhäuser mountains (Germany). *Acta Zoologica Fennica*, **195**, 124–8.
- Schultz, P.A. (1991). Grazing preference of two collembolan species, *Folsomia candida* and *Proisotoma minuta*, for ectomycorrhizal fungi. *Pedobiologia*, **35**, 313–25.
- Schwarz, A.M.J., Green, J.D., Green, T.G.A., and Seppelt, R.D. (1993). Invertebrates associated with moss communities at Canada Glacier, Southern Victoria Land, Antarctica. *Polar Biology*, **13**, 157–62.
- Scott, H.G. (1965). The Collembola of New Mexico. XV. Dicyrtominae. *Entomological News*, **76**, 129–31.
- Scott, H.G. (1966). Insect pests. Part 1. Springtails. *Modern Maintenance Management*, **18**, (9), 19–21.
- Scott, H.G., Wiseman, J.S., Stojanovich, C.J. (1962). Collembola infesting Man. *Annals of the Entomological Society of America*, **55**, 428–30.
- Seastedt, T.R. (1984). The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology*, **29**, 25–46.
- Seastedt, T.R. and Crossley, D.A. (1980). Effects of microarthropods on the seasonal dynamics of nutrients in forest litter. *Soil Biology and Biochemistry*, **12**, 337–42.
- Seastedt, T.R., Reddy, M.V., and Cline, S.P. (1989). Microarthropods in decaying wood from temperate coniferous and deciduous forests. *Pedobiologia*, **33**, 69–77.

- Sedlag, U. (1952). Untersuchungen über den Ventraltubus der Collembolen. *Wissenschaftliche Zeitschrift der Martin-Luther-Universität Halle-Wittenburg*, **1**, 93–127.
- Seifert, R.P., Beaman, N.J., Broadus, E.B., and Schwartz, J.A. (1981). The intrinsic rate of natural increase of *Willowsia nigromaculata* (Lubbock) (Collembola, Entomobryidae). *Journal of the Kansas Entomological Society*, **54**, 748–50.
- Selga, D. (1966). Anuroforinos de la Península Ibérica (Collembola). *Boletín de la Real Sociedad Española de Historia Natural (Biológica)*, **64**, 335–50.
- Selga, D. (1971). Catálogo de los Colémbolos de la Península Ibérica. *Graellsia*, **26**, 133–284.
- Setälä, H. (1995). Growth of birch and pine seedlings in relation to grazing by soil fauna on ectomycorrhizal fungi. *Ecology*, **76**, 1844–51.
- Setälä, H. and Marshall, V.G. (1993). Succession of Collembola in stumps of Douglas fir seres representing clear-cuts to old-growth forest. In *Proceedings of the forest ecosystem dynamics workshop* (ed. V.G. Marshall), pp. 21–2. Forestry Canada, British Columbia.
- Setälä, H. and Marshall, V.G. (1994). Stumps as a habitat for Collembola during succession from clear-cut to old-growth Douglas fir forests. *Pedobiologia*, **38**, 307–26.
- Setälä, H., Marshall, V.G., and Trofymow, J.A. (1995). Influence of micro- and macro-habitat factors on Collembolan communities in Douglas fir stumps during forest succession. *Applied Soil Ecology*, **2**, 227–42.
- Sgardelis, S.P., Sarkar, S., Asikidis, M.D., Cancela de Fonseca, J.P., and Stamou, G.P. (1993). Phenological patterns of soil microarthropods from three climate regions. *European Journal of Soil Biology*, **29**, 49–57.
- Shan-Xiang, L. (1980). A new subfamily and a new genus of Onychiuridae (Collembola). *Acta Entomologica Sinica*, **23**, 188–90.
- Sharma, G.D. (1967). Bionomics of *Tomocerus vulgaris* Tullberg (Collembola, Entomobryidae). *Proceedings of the Royal Entomological Society of London*, **42A**, 30–4.
- Shaw, G. (1806). *General zoology or systematic natural history*. G. Kearsley, London.
- Shaw, P.J.A. (1985). Grazing preferences of *Onychiurus armatus* (Insecta: Collembola) for mycorrhizal and saprophytic fungi of pine plantations. In *Ecological interactions in soil: plants, microbes and animals* (eds. A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher) pp. 333–7. Blackwell, Oxford.
- Shaw, P.J.A. (1988). A consistent hierarchy in the fungal feeding preferences of the Collembola *Onychiurus armatus*. *Pedobiologia*, **31**, 179–87.
- Shear, W.A. (1992a). End of the 'Uniramia' taxon. *Nature*, **359**, 477–8.
- Shear, W.A. (1992b). Les premiers écosystèmes terrestres. *La Recherche*, **23**, 1258–67.
- Shear, W.A. and Kukalová-Peck, J. (1990). The ecology of Paleozoic terrestrial arthropods: the fossil evidence. *Canadian Journal of Zoology*, **68**, 1807–34.
- Shoebottom, J.W. (1917). Notes on Collembola. Part 4. The classification of the Collembola; with a list of genera known to occur in the British Isles. *Annals and Magazine of Natural History*, Series 8, **19**, 425–36.
- Siepel, H. (1990). Decomposition of leaves of *Avenella flexuosa* and microarthropod succession in grazed and ungrazed grasslands. I. Succession of microarthropods. *Pedobiologia*, **34**, 19–30.
- Siepel, H. (1994a). Life-history tactics of Collembola; an alternative to Gisin's life forms? *Acta Zoologica Fennica*, **195**, 129–31.
- Siepel, H. (1994b). *Structure and function of soil microarthropod communities*. PhD thesis, University of Wageningen.
- Siepel, H. (1995). Applications of microarthropod life-history tactics in nature management and ecotoxicology. *Biology and Fertility of Soils*, **19**, 75–83.
- Siepel, H. and Van de Bund, C.F. (1988). The influence of management practices on the microarthropod community of grassland. *Pedobiologia*, **31**, 339–54.
- Siepel, H. and Van Wieren, S.E. (1990). Decomposition of leaves of *Avenella flexuosa* and microarthropod succession in grazed and ungrazed grasslands. II. Chemical data and comparison of decomposition rates. *Pedobiologia*, **34**, 31–6.
- Sievers, H. and Ulber, B. (1990). The effects of organic manure applications on Collembola and other small arthropods as seedling pests in sugar beet. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz*, **97**, 588–99.
- Signor, P.W. (1994). Biodiversity in geological time. *American Zoologist*, **34**, 23–32.
- Simon, J.C. and Jordana, R. (1994). *Wankeliella medialis*, nueva especie para la fauna Ibérica (Collembola, Tullbergiinae). *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **24**, 15–18.
- Simón-Benito, J.C. and Lucíañez-Sánchez, M.J. (1990a). Estudio colembológico de diferentes pastizales de la Sierra de Ayllón, con descripción de dos nuevas especies (Insecta, Collembola). *Eos*, **66**, 67–77.
- Simón-Benito, J.C. and Lucíañez-Sánchez, M.J. (1990b). *Scaphaphorura corpesiensis* nov.sp. del Macizo de Ayllón, Guadalajara (Collembola: Tullbergiinae). *Graellsia*, **46**, 157–60.

- Simon, J.C. and Lucianez, M.J. (1994). Nuevas especies de la subfamilia Onychiurinae de la Península Ibérica. *Publicaciones de Biología de la Universidad de Navarra, Serie Zoológica*, **24**, 61–74.
- Simon-Benito, J.C. and Pozo-Martínez, J. (1984). Contribución al conocimiento del género *Microgastrura* Stach, 1922 (Collembola). *Nouvelle Revue d'Entomologie*, **1**, 267–76.
- Simon-Benito, J.C. and Pozo-Martínez, J. (1988). Colémbolos de Cantabria. *Eos*, **64**, 203–15.
- Simón, J.C., Bach, C. and Gaju, M. (1987). Colémbolos de la provincia de Córdoba (España) (Nota I). *Eos*, **62**, 297–306.
- Simon, J.C., Ruiz, M., Martín, J., and Lucíañez, M.J. (1994). Descripción de dos nuevos taxones *Mesaphorura florum* n.sp. y *Mesaphorura arbei* n.sp. (Collembola, Tullbergiinae) de la Sierra de Guadarrama. *Nouvelle Revue d'Entomologie*, **11**, 61–6.
- Singh, S.B. (1970). A preliminary observation on the gut contents of *Neanura muscorum* (Templeton) (Collembola, Neanuridae). *Entomologist's Monthly Magazine*, **106**, 85–7.
- Sinha, P.B., Sen, N.S., and Jafri, H.A. (1988). On the seasonal population fluctuations of Collembola and Acarina in a deciduous forest at Ranchi. *Journal of Environmental Biology*, **9**, 79–83.
- Skarzynski, D. (1991). Diagnostic value of morphological characters in *Onychiurus* (*Onychiurus*) *cebennarius* Gisin, 1956 (Collembola, Onychiuridae). *Polskie Pismo Entomologiczne*, **61**, 55–67.
- Skarzynski, D. and Pomorski, R.J. (1994). *Paranurida kopetdagi* a new genus and species of Neanuridae from Turkmenia (Insecta: Collembola). *Genus (Wroclaw)*, **5**, 363–6.
- Skidmore, R.E. (1995). Checklist of Collembola (Insecta: Apterygota) of Canada and Alaska. *Proceedings of the Entomological Society of Ontario*, **126**, 45–76.
- Slifer, E.H. and Sekhon, S.S. (1978). Sense organs on the antenna of two species of Collembola (Insecta). *Journal of Morphology*, **157**, 1–20.
- Smith, J.A. and Ross, W.D. (1910). *The works of Aristotle. Translated into English*. Clarendon Press, Oxford (Vol. IV. *Historia Animalium*, translated by D'Arcy Wentworth Thompson).
- Snider, R.J. (1967a). An annotated list of the Collembola (springtails) of Michigan. *Michigan Entomologist*, **1**, 179–234.
- Snider, R.J. (1967b). The chaetotaxy of North American *Lepidocyrtus* s.str. (Collembola: Entomobryidae). *Contributions of the American Entomological Institute*, **2**, 1–28.
- Snider, R.J. (1969a). New species of *Deuterostminthurus* and *Sminthurus* from Michigan (Collembola: Sminthuridae). *Revue d'Écologie et de Biologie du Sol*, **3**, 357–76.
- Snider, R.J. (1969b). *Polykatianna batchi*: a new species for North America (Collembola: Sminthuridae). *Michigan Entomologist*, **1**, 371–5.
- Snider, R.J. (1971). Dietary influence on the growth and fecundity of *Onychiurus justus* (Denis) (Onychiuridae: Collembola). *Annales de Zoologie, Ecologie Animale*, **1971**, 225–34.
- Snider, R.M. (1973). Laboratory observations on the biology of *Folsomia candida* (Willem) (Collembola: Isotomidae). *Revue d'Écologie et de Biologie du Sol*, **10**, 103–24.
- Snider, R.J. (1977). Development of instar chaetotaxy of *Onychiurus* (*Onychiurus*) *folsomi*. *Transactions of the American Microscopical Society*, **96**, 355–62.
- Snider, R.J. (1978). New species of Sminthuridae from North America (Collembola: Symphypleona). *Great Lakes Entomologist*, **11**, 217–41.
- Snider, R.J. (1981a). *Pseudachorutes* (*Pseudachorutes*) *quadrissetosus*, a new species of Collembola from Florida (Hypogastruridae: Neanurinae). *Florida Entomologist*, **64**, 244–6.
- Snider, R.J. (1981b). *Sminthurus carolinensis*, a new species from South Carolina (Collembola: Sminthuridae). *Florida Entomologist*, **64**, 417–24.
- Snider, R.J. (1981c). A new species of *Janetschekbrya* from Costa Rica (Collembola: Entomobryidae). *Entomological News*, **92**, 39–41.
- Snider, R.J. (1981d). *Bourletiella* (*Bourletiella*) *gibbonsi*, a new species from South Carolina (Collembola: Sminthuridae). *Entomological News*, **92**, 93–7.
- Snider, R.J. (1982a). Redescription of *Sminthurus floridanus* MacGillivray, 1893 (Collembola: Sminthuridae). *Florida Entomologist*, **65**, 221–7.
- Snider, R.J. (1982b). *Sminthurus fischeri*, a new species from Georgia (Collembola: Sminthuridae). *Florida Entomologist*, **65**, 321–6.
- Snider, R.J. (1983a). Observations on the oviposition, egg development and fecundity of *Onychiurus* (*Onychiurus*) *folsomi* at constant temperature. *Pedobiologia*, **25**, 241–52.
- Snider, R.J. (1983b). *Sminthurus mendenbergae*, new species from Canada and Michigan (Collembola: Sminthuridae). *Great Lakes Entomologist*, **16**, 115–22.
- Snider, R.J. (1985a). *Dicyrtoma* (*Ptenothrix*) *renateae*, new species from the Savannah River Plant and Georgia (Collembola: Dicyrtominae). *Florida Entomologist*, **68**, 561–6.
- Snider, R.J. (1985b). *Vesicephalus crossleyi*, new species from the Savannah River Plant and Georgia (Collembola: Sminthurinae). *Florida Entomologist*, **68**, 567–74.

- Snider, R.J. (1985c). *Sminthurus bivittatus*, new species from the Southeastern United States (Collembola: Sminthuridae). *Florida Entomologist*, **68**, 574–82.
- Snider, R.J. (1985d). *Dicyrtoma (Ptenothrix) castanea*, new species from the Savannah River Plant (Collembola: Dicyrtominae). *Florida Entomologist*, **68**, 582–7.
- Snider, R.J. (1987). Class and Order Collembola. In *Immature insects* (ed. F.W. Stehr), pp. 55–64. Kendall/Hunt, Dubique, Iowa.
- Snider, R.J. (1988a). A new species of Collembola from Utah (Collembola: Katiannidae). *Entomological News*, **99**, 1–6.
- Snider, R.J. (1988b). *Tritosminthurus schuhi*, a new genus and species from Cape Province, South Africa (Collembola: Bourletiellidae). *Entomological News*, **99**, 260–6.
- Snider, R.J. (1988c). *Denisiella lithophila*, a new species from a granite outcrop in Georgia (Collembola: Sminthuridae). *Florida Entomologist*, **71**, 125–9.
- Snider, R.J. (1989). Link between *Sminthurus* and *Katianna* collected from Alabama (Collembola: Katiannidae). *Florida Entomologist*, **72**, 541–7.
- Snider, R.J. (1990a). A contribution to the Dicyrtomidae (Collembola) of Hawaii. *Zoologica Scripta*, **19**, 73–99.
- Snider, R.J. (1990b). A new species of *Ptenothrix* and records from the Southeastern United States (Dicyrtomidae: Collembola). *Florida Entomologist*, **73**, 248–57.
- Snider, R.J. and Butcher, J.W. (1972). Response of *Onychiurus justus* (Denis) (Collembola: Onychiuridae) to constant temperatures and variable relative humidity. In *Proceedings of the First Soil Microcommunities Conference*, USAEC, Syracuse, New York. pp. 176–84.
- Snider, R.J. and Butcher, J.W. (1973). The life history of *Folsomia candida* (Willem) (Collembola: Isotomidae) relative to temperature. *Great Lakes Entomologist*, **6**, 97–106.
- Snider, R.J. and Calandrino, F.J. (1987). An annotated list and new species descriptions of Collembola found in the Project EFL study area of Michigan. *Great Lakes Entomologist*, **20**, 1–19.
- Snider, R.J. and Fischer, R.L. (1964). A Palearctic springtail, *Lepidocyrtus paradoxus* Uzel, found in North America (Collembola; Mydontidae). *Transactions of the American Microscopical Society*, **83**, 86–9.
- Snider, R.J. and Husband, R.W. (1966). Collembola found in bumblebee nests. *Transactions of the American Microscopical Society*, **85**, 473–5.
- Snider, R.J. and Loring, S.J. (1982). *Sminthurus incognitus*, new species from Florida (Collembola: Sminthuridae). *Florida Entomologist*, **65**, 216–21.
- Snider, R.J. and Loring, S.J. (1984). Occurrence and external morphology of proprioceptors (oval organs) among North American Sminthurinae (Collembola: Sminthuridae). *Annales de la Société Royale Zoologique de Belgique*, **114**, 35–42.
- Snider, R.J., Shaddy, J.H., and Butcher, J.W. (1969). Culture techniques for rearing soil arthropods. *Michigan Entomologist*, **1**, 357–62.
- Snider, R.J., Snider, R., and Smucker, A.J.M. (1990). Collembolan populations and root dynamics in Michigan agroecosystems. In *Rhizosphere dynamics* (ed. J.E. Box and L.C. Hammond), pp. 168–91. American Association for the Advancement of Science, Selected Symposium No. 113.
- Sømme, L. (1981a). Supercooling in two Antarctic terrestrial arthropods from Bouvetøya. *Norsk Polarinstitutt Skrifter*, **175**, 37–40.
- Sømme, L. (1981b). Cold tolerance of Alpine, Arctic and Antarctic Collembola and mites. *Cryobiology*, **18**, 212–20.
- Sømme, L. (1982). Supercooling and winter survival in terrestrial arthropods. *Comparative Biochemistry and Physiology*, **73A**, 519–43.
- Sømme, L. (1985). Ecological studies on *Cryptopygus sverdrupi* from Mühlig-Hofmannfjella, Antarctica. *Cryo Letters*, **6**, 392–3.
- Sømme, L. (1986a). Ecology of *Cryptopygus sverdrupi* (Insecta: Collembola) from Dronning Maud Land, Antarctica. *Polar Biology*, **6**, 179–84.
- Sømme, L. (1986b). Terrestrial arthropods of Bouvetøya. *Polar Research*, **4**, 231–3.
- Sømme, L. (1989). Adaptations of terrestrial arthropods to the alpine environment. *Biological Reviews*, **64**, 367–407.
- Sømme, L. (1993). Living in the cold. Insects and other terrestrial arthropods in alpine and polar areas. *Biologist*, **40**, 14–17.
- Sømme, L. (1994). The adaptation of alpine terrestrial arthropods to desiccation. *Acta Oecologia*, **15**, 55–62.
- Sømme, L. and Block, W. (1982). Cold hardiness of Collembola at Signy Island, maritime Antarctic. *Oikos*, **38**, 168–76.
- Sorensen, F.F., Bayley, M., and Baatrup, E. (1995). The effects of sublethal dimethoate exposure on the locomotor behaviour of the collembolan *Folsomia candida* (Isotomidae). *Environmental Toxicology and Chemistry*, **14**, 1587–90.

- Soto-Adames, F.N.S. (1987). A new species of *Actaetes* from Mexico (Collembola, Actaletidae). *Pan Pacific Entomologist*, **63**, 52–5.
- Soto-Adames, F.N. (1988a). Nuevos dicirtómidos de Puerto Rico (Insecta: Collembola: Dicyrtomidae). *Caribbean Journal of Science*, **24**, 60–70.
- Soto-Adames, F.N. (1988b). Revision de la familia Actaletidae Börner, 1902 (Insecta, Collembola). *Caribbean Journal of Science*, **24**, 161–96.
- Soto-Adames, F.N., Robertson, H.M., and Berlocher, S.H. (1994). Phylogenetic utility of partial DNA sequences of *G6 pdh* at different taxonomic levels in Hexapoda with emphasis on Diptera. *Annals of the Entomological Society of America*, **87**, 723–36.
- South, A. (1961). The taxonomy of the British species of *Entomobrya*. *Transactions of the Royal Entomological Society of London*, **113**, 387–416.
- Spahr, H.J. (1981). The importance of Collembola for soil biology and their suitability as test organisms for ecotoxicology. *Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz*, **54**, 27–9.
- Stach, J. (1926). *Spinisotoma pectinata* n.g., n.sp., eine neue interessante Gattung der Familie Isotomidae. *Bulletin de l'Académie Polonaise des Sciences et des Lettres, Série B*, 579–88.
- Stach, J. (1947). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Family Isotomidae. *Acta Monographica Musei Historiae Naturalis, Krakow*, **1947**, 1–488.
- Stach, J. (1949a). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Families Neogastruridae and Brachystomellidae. *Acta Monographica Musei Historiae Naturalis, Krakow*, **1949A**, 1–341.
- Stach, J. (1949b). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Families Anuridae and Pseudachorutidae. *Acta Monographica Musei Historiae Naturalis, Krakow*, **1949B**, 1–122.
- Stach, J. (1951). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Family Bilobidae. *Acta Monographica Musei Historiae Naturalis, Krakow*, **1951**, 1–97.
- Stach, J. (1954). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Family Onychiuridae. *Polska Akademia Nauk Instytut Zoologiczny, Krakow*, **1954**, 1–219.
- Stach, J. (1956). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Family Sminthuridae. *Polska Akademia Nauk Instytut Zoologiczny, Krakow*, **1956**, 1–287.
- Stach, J. (1957). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Families Neelidae and Dicyrtomidae. *Polska Akademia Nauk Instytut Zoologiczny, Krakow*, **1957**, 1–113.
- Stach, J. (1960a). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Tribe Orchesellini. *Polska Akademia Nauk Instytut Zoologiczny, Krakow*, **1960**, 1–151.
- Stach, J. (1960b). Materialien zur Kenntnis der Collembolen fauna Afghanistans. *Acta Zoologica Cracoviensia*, **5**, 507–81.
- Stach, J. (1961). The problem of the genus *Spinisotoma*. *Acta Zoologica Cracoviensia*, **5**, 715–24.
- Stach, J. (1963a). The apterygoten fauna of Poland in relation to the world fauna of this group of insects. Tribe Entomobryini. *Polska Akademia Nauk, Zakład Zoologii Systematycznej W Krakowie*, **1963**, 1–126.
- Stach, J. (1963b). Materialien zur Kenntnis der Collembolen fauna Afghanistans. II. Teil. *Acta Zoologica Cracoviensia*, **8**, 337–49.
- Stach, J. (1964a). Owady bezskrzydłe: Apterygota. In *Katalog Fauny Polski*, Vol. 15, pp. 1–103. Warszawa.
- Stach, J. (1964b). Materials to the knowledge of Chinese Collembolan fauna. *Acta Zoologica Cracoviensia*, **9**, 1–26.
- Stach, J. (1965). On some Collembola of North Vietnam. *Acta Zoologica Cracoviensia*, **10**, 345–72.
- Stach, J. (1967). Collembola fauna of Malta. *Acta Zoologica Cracoviensia*, **12**, 393–418.
- Stamou, G.P., Asikidis, M.D., Argyropoulou, M.D., and Sgardelis, S.P. (1993). Ecological time versus standard clock time: the asymmetry of phenologies and the life history strategies of some soil arthropods from Mediterranean ecosystems. *Oikos*, **66**, 27–35.
- Stark, J.D. (1992). Comparison of the impact of a neem seed-kernel extract formulation 'Margosan-O' and chlorpyrifos on non-target invertebrates inhabiting turf grass. *Pesticide Science*, **36**, 293–9.
- Stebaeva, S.K. (1989a). Role of Collembola in organic matter decomposition in technogenic Siberian landscapes. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 299–306. University of Siena, Siena.
- Stebaeva, S.K. (1989b). Landscape-zonal ecological niche of *Xenylla* species in the USSR. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 405–12. University of Siena, Siena.
- Stebaeva, S.K. and Grishina, L.G. (1983). Dynamics of microarthropods (Collembola, Oribatei) in the nest of *Formica polyctena* in the forest steppe of West Siberia. *Zoologicheskij Zhurnal*, **62**, 850–60.
- Steiner, W.A. (1994). The influence of air pollution on moss-dwelling animals. 1. Methodology and composition of flora and fauna. *Revue Suisse de Zoologie*, **101**, 533–56.

- Steiner, W.A. (1995). Influence of air pollution on moss dwelling animals. 3. Terrestrial fauna, with emphasis on Oribatida and Collembola. *Acarologia*, **36**, 149–73.
- Stenton, R. (1922). Springtails attacking mangolds. *Journal of the Ministry of Agriculture*, **29**, 828–9.
- Sterzynska, M. (1989). Collembola from urban areas (Warsaw, Poland). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 347–54. University of Siena, Siena.
- Sterzynska, M. (ed.) (1995). Fourth Seminar on Apterygota. *Polskie Pismo Entomologiczne*, **64**, 1–420.
- Stevenson, B.G. and Dindal, D.L. (1982). Effect of leaf shape on forest litter Collembola: community organization and microhabitat selection of two species. *Journal of the Georgia Entomological Society*, **17**, 363–9.
- Stomp, N. (1971). Contribution à l'étude des *Pseudosinella* endogés espèces européennes de *Pseudosinella* à 5 + 5 yeux (Collembola, Entomobryidae). *Revue d'Écologie et de Biologie du Sol*, **8**, 173–88.
- Stomp, N. (1974). Collembolles cavernicoles d'Afrique du Nord (Insecta). I. *Annales de Spéléologie*, **29**, 109–20.
- Stomp, N. (1983). Collembolles cavernicoles d'Afrique du Nord (Insecta). II. *Revue Suisse de Zoologie*, **90**, 191–8.
- Stomp, N. (1986). Le groupe de *Pseudosinella vandeli* (Insectes, Collembolles) dans les Alpes Orientales. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 85–91. University of Siena, Siena.
- Stomp, N. and Weiner, W.M. (1994). Redescription of *Plutomurus unidentatus* (Börner, 1901) comb.nov. (Collembola, Tomoceridae). *Bulletin Société des Naturalistes Luxembourgeois*, **95**, 359–64.
- Stomp, N., Massoud, Z., and Thibaud, J.M. (1982). Insectes Collembolles de quelques départements du Sud de la France. *Nouvelle Revue d'Entomologie*, **12**, 9–24.
- Stomp, N., Tommasi-Ursone, M.L., and Christian, E. (1991). Description et redescription de quelques espèces de *Pseudosinella cavernicoles* de l'Autriche (Insectes, Collembolles). *Bulletin Société des Naturalistes Luxembourgeois*, **92**, 121–30.
- Storey, B.C. (1995). The role of mantle plumes in continental break up: case histories from Gondwanaland. *Nature*, **377**, 301–8.
- Stork, N.E. (1988). Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society*, **35**, 321–37.
- Stork, N.E. and Blackburn, T.M. (1993). Abundance, body size and biomass of arthropods in tropical forest. *Oikos*, **67**, 483–9.
- Stork, N.E. and Eggleton, P. (1992). Invertebrates as determinants and indicators of soil quality. *American Journal of Alternative Agriculture*, **7**, 23–32.
- Streit, B. (1992). Bioaccumulation processes in ecosystems. *Experientia*, **48**, 955–70.
- Strojan, C.L. (1978). The impact of zinc smelter emissions on forest litter arthropods. *Oikos*, **31**, 41–6.
- Stys, P. and Bilinski, S. (1990). Ovariole types and the phylogeny of hexapods. *Biological Reviews*, **65**, 401–29.
- Subagia, J. and Snider, R.J. (1981). The side effects of the herbicides atrazine and paraquat upon *Folsomia candida* and *Tullbergia granulata* (Insecta, Collembola). *Pedobiologia*, **22**, 141–52.
- Sugawara, H., Higasi, S., and Fukuda, H. (1987). Entomological and ecological surveys on Mt. Usu in 1984. VI. Faunal make-up and ecological distribution of springtails (Collembola) on volcano Usu. *Ecological Research*, **2**, 121–32.
- Suhardjono, Y.R. (1989a). Revised checklist of Collembola from Indonesia and its adjacent regions. *Acta Zoologica Asiae Orientalis*, **1**, 1–22.
- Suhardjono, Y.R. (1989b). Isotomidae from Indonesia. I. *Acta Zoologica Asiae Orientalis*, **1**, 119–27.
- Suhardjono, Y.R. and Deharveng, L. (1992). *Siamanura primadinae*, a new species of Neanurinae (Collembola, Neanuridae) from East Java, Indonesia. *Raffles Bulletin of Zoology*, **40**, 61–4.
- Suhardjono, Y.R. and Greenslade, P. (1994). *Folsomides arnoldi* n.sp. (Isotomidae): a new Collembolan abundant in arid Australia, with a redescription of *Folsomides denisi* (Womersley). *Proceedings of the Linnean Society of New South Wales*, **114**, 21–7.
- Suma, Y. (1981). A new humicolous species of *Plutomurus* (Collembola, Tomoceridae) from Hokkaido, North Japan. *Kontyu, Tokyo*, **49**, 502–5.
- Sustr, V. and Simek, M. (1994). Environmental factors influencing respiration of the stenothermic collembolan *Tetrodonthophora bielensis* (Entognatha, Collembola). *Pedobiologia*, **38**, 63–71.
- Swammerdam, J. (1737–1738). *Bybel der nature, of historie der insecten. Biblia naturae; sive historia insectorum. Isaak Severinus, Boudewya Van der Aa, Pieter Van der Aa, Leiden*. 2 vols.
- Szeptycki, A. (1967a). Morpho-systematic studies on Collembola. Part 1. Materials to a revision of the genus *Lepidocyrtus* Bourlet, 1839 (Entomobryidae s.l.). *Acta Zoologica Cracoviensis*, **12**, 369–77.
- Szeptycki, A. (1967b). Fauna of the springtails (Collembola) of the Ojców National Park in Poland. *Acta Zoologica Cracoviensis*, **12**, 219–80.

- Szeptycki, A. (1969). Morpho-systematic studies on Collembola. II. Postembryonic development of the chaetotaxy in *Entomobryoides myrmecophila* (Reuter, 1886). *Acta Zoologica Cracoviensia*, **14**, 163–72.
- Szeptycki, A. (1972). Morpho-systematic studies on Collembola. III. Body chaetotaxy in the first instars of several genera of the Entomobryomorpha. *Acta Zoologica Cracoviensia*, **17**, 341–72.
- Szeptycki, A. (1973). North Korean Collembola. I. The genus *Homidia* Börner 1906 (Entomobryidae). *Acta Zoologica Cracoviensia*, **18**, 23–39.
- Szeptycki, A. (1976). Jan Waclaw Stach 1877–1975. *Pedobiologia*, **16**, 396–7.
- Szeptycki, A. (1977a). Morpho-systematic studies on Collembola. V. The body chaetotaxy of the genera *Oncopodura* Carl et Lebedinsky, 1905 and *Harlomillsia* Bonet, 1944 (Oncopoduridae). *Revue d'Écologie et de Biologie du Sol*, **14**, 199–209.
- Szeptycki, A. (1977b). North Korean Collembola. II. The genus *Oncopodura* Carl et Lebedinsky, 1905 (Oncopoduridae). *Acta Zoologica Cracoviensia*, **22**, 45–54.
- Szeptycki, A. (1979). Chaetotaxy of the Entomobryidae and its phylogenetical significance. Morpho-systematic studies on Collembola. IV. *Polska Akademia Nauk Instytut Zoologiczny, Krakow*, **1979**, 1–218.
- Szeptycki, A. and Weiner, W.M. (1990). Collembola – Skoczogonki. In *Checklist of the animals of Poland*, Vol. 1, Part 32 (1–20), (ed. J. Razowski), pp. 19–27. Wrocklaw-Warszawa-Krakow.
- Szklarzewicz, T. and Klag, J. (1986). Cytochemical analysis of nuage in freshly formed primordial germ cells of *Tetradontophora bielensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **28**, 1.
- Takeda, H. (1976). Ecological studies of collembolan populations in a pine forest soil. I. The life cycle and population dynamics of *Tetracanthella sylvatica* Yosii. *Revue d'Écologie et de Biologie du Sol*, **13**, 117–32.
- Takeda, H. (1978). Ecological studies of collembolan populations in a pine forest soil. II. Vertical distribution of Collembola. *Pedobiologia*, **18**, 22–30.
- Takeda, H. (1979a). Ecological studies of collembolan populations in a pine forest soil. III. The life cycles and population dynamics of some surface dwelling species. *Pedobiologia*, **19**, 34–47.
- Takeda, H. (1979b). On the extraction process and efficiency of MacFadyen's high gradient extractor. *Pedobiologia*, **19**, 106–12.
- Takeda, H. (1979c). Ecological studies of collembolan populations in a pine forest soil. IV. Comparison of distribution patterns. *Researches on Population Ecology*, **21**, 120–34.
- Takeda, H. (1981). Effects of shifting cultivation on the soil meso-fauna with special reference to collembolan populations in N.E. Thailand. *Memoirs of the College of Agriculture, Kyoto University*, **118**, 45–60.
- Takeda, H. (1983). A long term study of life cycles and population dynamics of *Tullbergia yosii* and *Onychiurus decemsetosus*. *Pedobiologia*, **25**, 175–85.
- Takeda, H. (1984). A long term study of life cycle and population dynamics of *Folsomia octoculata* Handschin (Insecta: Collembola) in a pine forest soil. *Researches on Population Ecology*, **26**, 188–219.
- Takeda, H. (1985). A note on ecomorphosis in *Folsomia octoculata* Handschin (Insecta: Collembola). *Edaphologia*, **32**, 29–33.
- Takeda, H. (1987). Dynamics and maintenance of collembolan community structure in a forest soil system. *Researches on Population Ecology*, **29**, 291–346.
- Takeda, H. (1988). A 5 year study of pine needle litter decomposition in relation to mass loss and faunal abundances. *Pedobiologia*, **32**, 221–6.
- Takeda, H. (1995). Changes in the Collembolan community during the decomposition of needle litter in a coniferous forest. *Pedobiologia*, **39**, 304–17.
- Takeda, H. and Ichimura, T. (1983). Feeding attributes of four species of Collembola in a pine forest soil. *Pedobiologia*, **25**, 373–81.
- Tamarelle, M. (1979). Recherches ultrastructurales sur la ségrégation et de développement de la lignée germinale chez les embryons de quatre collembolles (Insecta: Apterygota). *International Journal of Insect Morphology and Embryology*, **8**, 95–111.
- Tamarelle, M. (1981). La formation et l'évolution de l'organe dorsal chez les embryons de cinq collembolles (Insecta: Apterygota). *International Journal of Insect Morphology and Embryology*, **10**, 203–24.
- Tamarelle, M. (1984). Transient rudiments of second antennae on the intercalary segment of embryos of *Anurida maritima* Guer (Collembola, Arthropleona) and *Hyphantria cunea* Drury (Lepidoptera, Arctiidae). *International Journal of Insect Morphology and Embryology*, **13**, 331–6.
- Tamm, J.C. (1984). Surviving long submergence in the egg stage: a successful strategy of terrestrial arthropods living in flood plains (Collembola, Acari, Diptera). *Oecologia*, **61**, 417–9.
- Tamm, J.C. (1986a). Temperature-controlled underwater egg dormancy and postflood hatching in *Isotoma viridis* (Collembola) as forms of adaptation to annual long term flooding. *Oecologia*, **68**, 241–5.
- Tamm, J.C. (1986b). Fünfjährige Collembolensukzession auf einem verbrannten Kiefernwaldboden in Niedersachsen (BRD). *Pedobiologia*, **29**, 113–27.

- Tanaka, S. (1984). Studies on *Morulina* (Collembola, Neanuridae) from Japan. I. Two new species closely related to *Morulina triverrucosa* Tanaka. *Revue d'Écologie et de Biologie du Sol*, **21**, 127–43.
- Telford, M.J. and Thomas, R.H. (1995). Demise of the Atelocerata? *Nature*, **376**, 123–4.
- Terron-Sierra, R.A. and Palacios-Vargas, J.G. (1991). Colembolos atraídos a necrotrampas NTP-80 en la Reserva de la Biosfera 'La Michilia', Durango, Mexico. *Folia Entomológica Mexicana*, **81**, 337–9.
- Testerink, G.J. (1981). Starvation in a field population of litter-inhabiting Collembola. Methods for determining food reserves in small arthropods. *Pedobiologia*, **21**, 427–33.
- Testerink, G.J. (1982). Strategies in energy consumption and partitioning in Collembola. *Ecological Entomology*, **7**, 341–51.
- Testerink, G.J. (1983). Metabolic adaptations to seasonal changes in humidity and temperature in litter-inhabiting Collembola. *Oikos*, **40**, 234–40.
- Teuben, A. (1991). Nutrient availability and interactions between soil arthropods and microorganisms during decomposition of coniferous litter: a mesocosm study. *Biology and Fertility of Soils*, **10**, 256–66.
- Teuben, A. and Roelofsma, T.A.P.J. (1990). Dynamic interactions between functional groups of soil arthropods and microorganisms during decomposition of coniferous litter and microcosm experiments. *Biology and Fertility of Soils*, **9**, 145–51.
- Teuben, A. and Smidt, G.R.B. (1992). Soil arthropod numbers and biomass in two pine forests on different soils, related to functional groups. *Pedobiologia*, **36**, 79–89.
- Teuben, A. and Verhoef, H.A. (1992a). Relevance of micro- and mesocosm experiments for studying soil ecosystem processes. *Soil Biology and Biochemistry*, **24**, 1179–83.
- Teuben, A. and Verhoef, H.A. (1992b). Direct contribution by soil arthropods to nutrient availability through body and faecal nutrient content. *Biology and Fertility of Soils*, **14**, 71–5.
- Theobald, F.V. (1909). *The insect and other allied pests of orchard, bush and hothouse fruits and their prevention and treatment*. Published by the author, Wye.
- Theobald, F.V. (1910). Springtails (Collembola), their economic importance with notes on some unrecorded instances of damage. Report on economic zoology for the year ending 30th September, 1910. *Journal of the South Eastern Agricultural College, Wye*, **19**, 73–211 (Collembola on pp. 183–99).
- Thibaud, J.M. (1963). Documents sur le genre *Acherontiella* Absolon (Collembola) et description d'une espèce de Côte d'Ivoire. *Annales de Spéléologie*, **18**, 287–97.
- Thibaud, J.M. (1967). Contribution à l'étude du développement postembryonnaire chez les Collembolles Hypogastruridae épigés et cavernicoles (Première note). *Annales de Spéléologie*, **22**, 167–97.
- Thibaud, J.M. (1968a). Contribution à l'étude de l'action des facteurs température et humidité sur la durée du développement embryonnaire des Collembolles Hypogastruridae. *Revue d'Écologie et de Biologie du Sol*, **5**, 55–62.
- Thibaud, J.M. (1968b). Contribution à l'étude de l'action des facteurs température et humidité sur la durée du développement postembryonnaire et de l'intermue de l'adulte chez les Collembolles Hypogastruridae. *Revue d'Écologie et de Biologie du Sol*, **5**, 265–81.
- Thibaud, J.M. (1969). Contribution à l'étude du développement postembryonnaire chez les Collembolles Hypogastruridae épigés et cavernicoles (suite). *Revue d'Écologie et de Biologie du Sol*, **6**, 209–20.
- Thibaud, J.M. (1970). Biologie et écologie des Collembolles Hypogastruridae édaphiques et cavernicoles. *Mémoires du Muséum National d'Histoire Naturelle, Zoologie*, **61A**, 83–201.
- Thibaud, J.M. (1972). Révision du g. *Schaefferia* Absolon, 1900 (Insecte, Collembola). *Annales de Spéléologie*, **27**, 363–94.
- Thibaud, J.M. (1975). Données sur l'intermue et les températures léthales chez quelques espèces d'insectes Collembolles Poduromorphes. *Annales de Spéléologie*, **30**, 187–94.
- Thibaud, J.M. (1976a). Structure et régression de l'appareil oculaire chez les Insectes Collembolles. *Revue d'Écologie et de Biologie du Sol*, **13**, 173–90.
- Thibaud, J.M. (1976b). Relations chronologiques entre les cycles du tube digestif et de l'appareil génital lors de l'intermue des Insectes Collembolles. *Revue d'Écologie et de Biologie du Sol*, **13**, 191–204.
- Thibaud, J.M. (1977a). Intermue et températures léthales chez les Insectes Collembolles Arthropléones. I. Hypogastruridae et Onychiuridae. *Revue d'Écologie et de Biologie du Sol*, **14**, 45–61.
- Thibaud, J.M. (1977b). Intermue et températures léthales chez les Insectes Collembolles Arthropléones. II. Isotomidae, Entomobryidae et Tomoceridae. *Revue d'Écologie et de Biologie du Sol*, **14**, 267–78.
- Thibaud, J.M. (1980a). Croissances pondérale et linéaire chez les Insectes Collembolles. *Revue d'Écologie et de Biologie du Sol*, **17**, 405–18.
- Thibaud, J.M. (1980b). Révision des genres *Typhlogastrura* Bonet, 1930, et *Bonetogastrura* Thibaud, 1974 (Insectes, Collembolles). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **2A**, 245–87.
- Thibaud, J.M. (1981). Limite temporelle de résistance au jeûne partiel chez les Insectes Collembolles cavernicoles. *Revue d'Écologie et de Biologie du Sol*, **18**, 391–6.

- Thibaud, J.M. (1984a). Variations sur les Insectes Collemboles, particulièrement ceux d'Afrique du Nord et d'Égypte. *Cairo University of African Studies Reviews*, **9**, 1–8.
- Thibaud, J.M. (1984b). Mise au point sur la biogéographie des Insectes Collemboles de Bulgarie, particulièrement sur les cavernicoles. *Conférence Européenne Régionale de Spéléologie, Sofia, Bulgaria*, 1980, 146–53.
- Thibaud, J.M. (1986). Essai sur une classification biologique et écophysologique des Collemboles (Insectes) cavernicoles. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris, Série III*, **303**, 65–7.
- Thibaud, J.M. (1990). Révision du genre *Acherontiella* Absolon, 1913 (Insecta, Collembola). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **12A**, 401–14.
- Thibaud, J.M. (1991a). Les Collemboles des Petits Antilles. V. Considérations biogéographiques et écophysologiques sur les Collemboles Poduromorphs. *Revue d'Écologie et de Biologie du Sol*, **28**, 91–111.
- Thibaud, J.M. (1991b). Les insectes Collemboles particulièrement les cavernicoles. *Entomological Research Seminars, University of Korea, Seoul, Korea*, **12**, 13–20.
- Thibaud, J.M. (1992). Collemboles des sables littoraux d'Albanie et de Roumanie. *Revue Française d'Entomologie*, **14**, 21–3.
- Thibaud, J.M. (1993a). Les Collemboles des Petits Antilles. IV. Interstitiels terrestres et marins. *Revue Française d'Entomologie*, **15**, 69–80.
- Thibaud, J.M. (1993b). Sur les Collemboles des grottes de lave de l'Ile de Je Ju (Corée du Sud). *Mémoires de Biospéologie*, **20**, 255–6.
- Thibaud, J.M. (1994a). For a biological and ecological classification of cavernicolous Collembola (Hexapoda). *Mémoires de Biospéologie*, **21**, 147–9.
- Thibaud, J.M. (1994b). Les Collemboles interstitiels terrestres de l'Ile de Cuba, avec la description de deux espèces nouvelles. *Revue Française d'Entomologie*, **16**, 93–8.
- Thibaud, J.M. (1995a). Recherche sur la faune interstitielle aérienne des sables fins: les Collemboles littoraux de l'Hérault. *Annales de la Société Entomologique de France*, **31**, 31–7.
- Thibaud, J.M. (1995b). Une nouvelle espèce de *Schaefferia* d'une grotte des États-Unis d'Amérique (Collembola, Hypogastruridae). *Revue Française d'Entomologie*, **17**, 77–8.
- Thibaud, J.M. and Christian, E. (1986). Collemboles interstitiels aériens des sables d'Autriche. *Annales de la Société Entomologique de France*, **22**, 403–7.
- Thibaud, J.M. and Christian, E. (1989). Collemboles interstitiels aériens des sables littoraux méditerranéens. *Annales de la Société Entomologique de France*, **25**, 71–81.
- Thibaud, J.M. and Christian, E. (1991). Interstitielle Collembolen aus ungarischen Flugsand-Akkumulationen. *Opuscular Zoologica*, **24**, 159–65.
- Thibaud, J.M. and Deharveng, L. (1994). Collembola. In *Encyclopaedia biospeologica* (ed. C. Juberthie and V. Decu), pp. 267–76. Société de Biospéologie (CNRS), Moulis: Académie Roumaine, Bucarest.
- Thibaud, J.M. and Lee, B.H. (1994). Three new species of interstitial Collembola (Insecta) from sand dunes of South Korea. *Korean Journal of Systematic Zoology*, **10**, 39–46.
- Thibaud, J.M. and Massoud, Z. (1973a). Essai de classification des Insectes Collemboles 'cavernicoles' européens. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **277D**, 2137–40.
- Thibaud, J.M. and Massoud, Z. (1973b). Étude de la régression des cornéules chez les Insectes Collemboles. *Annales de Spéléologie*, **28**, 159–66.
- Thibaud, J.M. and Massoud, Z. (1977). Comparaison entre la faune des Collemboles épigés et cavernicoles de Ramioul (Belgique). *Nouvelle Revue d'Entomologie*, **7**, 5–7.
- Thibaud, J.M. and Massoud, Z. (1979). Les Collemboles des Petits Antilles. I. Hypogastruridae et Onychiuridae. *Revue d'Écologie et de Biologie du Sol*, **16**, 547–67.
- Thibaud, J.M. and Massoud, Z. (1980). Étude des Collemboles de certains milieux du Maroc et considérations biogéographiques sur la faune du Maghreb. *Revue Suisse de Zoologie*, **87**, 513–48.
- Thibaud, J.M. and Massoud, Z. (1983a). Un nouveau genre d'Insectes Collemboles Hypogastruridae cavernicole du Pays Basque. *Mémoires de Biospéologie*, **10**, 317–9.
- Thibaud, J.M. and Massoud, Z. (1983b). Les Collemboles des Petites Antilles. III. Neanuridae (Pseudochorutinae). *Revue d'Écologie et de Biologie du Sol*, **20**, 111–29.
- Thibaud, J.M. and Massoud, Z. (1986a). Insecta: Collembola. In *Stygofauna mundi*, pp. 616–7. E.J. Brill, Leiden.
- Thibaud, J.M. and Massoud, Z. (1986b). Un nouveau genre d'Insectes Collemboles Onychiuridae cavernicoles des Picos de Europa (Espagne). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **8A**, 327–31.
- Thibaud, J.M. and Massoud, Z. (1988). Recherche sur la faune interstitielle aérienne des sables fins: les Collemboles. II. Namib Desert. *Annales de la Société Entomologique de France, N.S.*, **24**, 211–4.

- Thibaud, J.M. and Najt, J. (1987). Collemboles (Insecta) de l'Équateur. II. Entomobryidae p.p., Cyphoderidae et Oncopoduridae. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **9A**, 933–46.
- Thibaud, J.M. and Najt, J. (1988). Collemboles (Insecta) de l'Équateur. IV. Paronellidae avec révision de quatre genres. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **10A**, 719–30.
- Thibaud, J.M. and Najt, J. (1989). Errata et addenda aux Collemboles (Insecta) de l'Équateur, II et IV. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **11A**, 983.
- Thibaud, J.M. and Najt, J. (1992). Isotogastruridae, a new family of terrestrial interstitial Collembola from the Lesser Antilles. *Bonner Zoologische Beiträge*, **43**, 545–51.
- Thibaud, J.M. and Najt, J. (1993). Les Collemboles (Insecta) de l'atoll de Fangataufa. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **15A**, 95–105.
- Thibaud, J.M. and Oliveira, E.P. de (1988). Durée des développements embryonnaire et postembryonnaire, intermue des adultes, en fonction de la température chez les Insectes Collemboles néotropicaux. *Revue d'Écologie et de Biologie du Sol*, **25**, 251–6.
- Thibaud, J.M. and Peja, N. (1994). Les Collemboles de la zone de Kabash (Pogradec) en Albanie. *Revue Française d'Entomologie*, **16**, 57–9.
- Thibaud, J.M. and Stomp, N. (1978). Collemboles cavernicoles et interstitiels du Département de l'Ardèche (France). *Nouvelle Revue d'Entomologie*, **8**, 3–15.
- Thibaud, J.M. and Vannier, G. (1969). Étude de l'action des facteurs température et humidité sur la durée de l'intermue de *Mesachorutes quadriocellatus* (Collembola: Hypogastruridae) et du concept de disponibilité en eau appliqué à une population de cette espèce guanoïde. *Annales de Spéléologie*, **24**, 613–8.
- Thibaud, J.M. and Vannier, G. (1978). Relations entre les tailles, les biomasses, les teneurs en eau et en lipides chez deux espèces de Collemboles selon leur répartition dans la grotte de Saint-Catherine (Ariège, France). *Revue d'Écologie et de Biologie du Sol*, **15**, 89–101.
- Thibaud, J.M. and Vannier, G. (1980). Diagrammes de transpiration chez les Collemboles Hypogastruridae en relation avec leur biotope. *Revue d'Écologie et de Biologie du Sol*, **17**, 41–52.
- Thibaud, J.M. and Vannier, G. (1986). Caractérisations biologique et ecophysiologique des Insectes Collemboles cavernicoles. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 129–37. University of Siena, Siena.
- Thibaud, J.M. and Weiner, W.M. (1994). *Psammophorura gedanica* g.n., sp.n. et autres Collemboles interstitiels terrestres de Pologne. *Polskie Pismo Entomologiczne*, **63**, 3–15.
- Thibaud, J.M., Najt, J., and Jaquemart, S. (1994). Les Collemboles (Insecta) de l'Archipel des Galápagos. II. Isotomidae. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie*, **64**, 199–204.
- Thibaud-Brauner, U. (1985). Electron microscopical investigations on the eye-structure and eye-reduction in the cavernicolous springtail *Bonetogastrura cavicola* (Insecta: Collembola). *Zoologischer Anzeiger*, **214**, 193–202.
- Thiele, A. and Larink, O. (1990). Colour marking in experiments on food selection with Collembola. *Biology and Fertility of Soils*, **9**, 203–4.
- Thimm, T. and Larink, O. (1995). Grazing preferences of some Collembola for endomycorrhizal fungi. *Biology and Fertility of Soils*, **19**, 266–8.
- Thome, J.P. and Desière, M. (1975). Évolution de la densité numérique des populations de Collemboles dans les excréments de Bovidés et d'Équidés. *Revue d'Écologie et de Biologie du Sol*, **12**, 627–41.
- Thompson, A.R. (1973). Persistence of biological activity of seven insecticides in soil assayed with *Folsomia candida*. *Journal of Economic Entomology*, **66**, 855–7.
- Thompson, A.R. and Gore, F.L. (1972). Toxicity of twenty nine insecticides to *Folsomia candida*: laboratory studies. *Journal of Economic Entomology*, **65**, 1255–60.
- Thompson, M. (1924). The soil population. An investigation of the biology of soil in certain districts of Aberystwyth. *Annals of Applied Biology*, **11**, 349–94.
- Tilbrook, P.J. and Block, W. (1972). Oxygen uptake in an Antarctic collembola, *Cryptopygus antarcticus*. *Oikos*, **23**, 313–7.
- Toda, J.M. and Tanno, K. (1983). The convergence of habitat structure in tundra collembolan communities (Insecta: Order Collembola). *Canadian Entomologist*, **115**, 1129–45.
- Tomlin, A.D. (1975). Toxicity of soil applications of insecticides to three species of springtails (Collembola) under laboratory conditions. *Canadian Entomologist*, **107**, 169–74.
- Tomlin, A.D. (1977). Toxicity of soil applications of the fungicide benomyl, and two analogues, to three species of Collembola. *Canadian Entomologist*, **109**, 1619–20.
- Topsel, E. (1658). *The history of four-footed beasts and serpents*. E. Cotes for G. Sawbridge, London.
- Tosi, L. (1977). Alimenti animali nelle diete di alcune specie di collemboli: ricerche preliminari sul cannibalismo in *Sinella coeca* (Schott). *Ateneo Parmense, Acta Naturi*, **13**, 445–55.

- Tosi, L. and Ferrari, R. (1989). Determination of the energy charge in two species of Collembola. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 437–42. University of Siena, Siena.
- Tosi, L. and Parisi, V. (1990). *Seira tongiorgii*, a new species of Collembola from a volcanic environment. *Bollettino di Zoologia*, **57**, 277–81.
- Tosi, L., Parisi, V., and Nieder, L. (1977). Analysis of the feeding behaviour of *Sinella coeca* (Schött) (Collembola). *Revue d'Écologie et de Biologie du Sol*, **14**, 483–92.
- Tranvik, L. and Eijsackers, H. (1989). On the advantage of *Folsomia finetarioides* over *Isotomiella minor* (Collembola) in a metal polluted soil. *Oecologia*, **80**, 195–200.
- Tranvik, L., Bengtsson, G., and Rundgren, S. (1993). Relative abundance and resistance traits of two Collembola species under metal stress. *Journal of Applied Ecology*, **30**, 43–52.
- Tranvik, L., Sjogren, M., and Bengtsson, G. (1994). Allozyme polymorphism and protein profile in *Orchesella cincta* (Collembola): indicative of extended metal pollution? *Biochemical Systematics and Ecology*, **22**, 13–23.
- Traser, G. and Christian, E. (1992). *Lepidocyrtus peisonis* sp.n., ein neuer Springschwanz aus dem Neusiedlersee-Gebiet (Collembola: Entomobryidae). *Folia Entomologica Hungarica*, **52**, 119–21.
- Traser, G., Thibaud, J.M., and Najt, J. (1993). Deux nouvelles espèces de Collembolles (Insecta) de Hongrie. *Bonner Zoologische Beiträge*, **44**, 221–4.
- Trockner, V. and Kopeszky, H. (1994). Auswirkungen der künstlichen Beschneidung auf Bodenverdichtung, Bodentemperatur, Ernteertrag und Collembolenfauna von Pistenböden. *Verhandlungen der Gesellschaft für Ökologie*, **23**, 283–8.
- Turner, B.D. (1983). Annual respiration and production estimates for collembolan and psocopteran epiphyte herbivores on larch trees in southern England. *Ecological Entomology*, **8**, 213–88.
- Tyszkiewicz, K. (1976). The embryogenesis of the central nervous system of *Tetrodontophora bielanensis* Waga (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **19**, 1–21.
- Tyszkiewicz, K. (1981). Anatomy and histology of brain of *Tetrodontophora bielanensis* (Waga) (Collembola). *Acta Biologica Cracoviensia, Zoologie*, **23**, 177.
- Uchida, H. (1971). Tentative key to the Japanese genera of Collembola, in relation to the World genera of this Order. I. *Scientific Reports of Hirosaki University*, **18**, 64–76.
- Uchida, H. (1972a). Tentative key to the Japanese genera of Collembola, in relation to the World genera of this Order. II. *Scientific Reports of Hirosaki University*, **19**, 19–42.
- Uchida, H. (1972b). Tentative key to the Japanese genera of Collembola, in relation to the World genera of this Order. III. *Scientific Reports of Hirosaki University*, **19**, 79–114.
- Uchida, H. and Chiba, S. (1958). Studies on the development of *Tomocerus minutus* Tullberg (Insecta: Collembola). I. On the postembryonic development. *Zoological Magazine (Tokyo)*, **67**, 242–8.
- Uchida, H. and Chiba, S. (1959). Studies on the development of *Tomocerus minutus* Tullberg (Insecta: Collembola). II. On the postembryonic development (later larval stages). *Zoological Magazine (Tokyo)*, **68**, 200–4.
- Uchida, H. and Hongo, T. (1962). Studies on the development of *Tomocerus minutus* Tullberg (Insecta: Collembola). III. Statistical analysis on the developmental stages. *Zoological Magazine (Tokyo)*, **71**, 91–7.
- Uemiyai, H. and Ando, H. (1987a). Blastodermic cuticles of a springtail *Tomocerus ishibashii* Yosii (Collembola: Tomoceridae). *International Journal of Insect Morphology and Embryology*, **16**, 287–94.
- Uemiyai, H. and Ando, H. (1987b). Embryogenesis of a springtail *Tomocerus ishibashii* (Collembola: Tomoceridae): external morphology. *Journal of Morphology*, **191**, 37–48.
- Uemiyai, H. and Ando, H. (1991). Mesoderm formation in a springtail *Tomocerus ishibashii* Yosii (Collembola, Tomoceridae). *International Journal of Insect Morphology and Embryology*, **20**, 283–90.
- Ulber, B. (1980). Untersuchungen zur Nahrungswahl von *Onychiurus fimatus* Gisin einem Aufgangschädling der Zuckerrübe. *Zeitschrift für Angewandte Entomologie*, **90**, 333–46.
- Upton, M.S. (1993). Aqueous gum-chloral slide mounting media: an historical review. *Bulletin of Entomological Research*, **83**, 267–74.
- Urbásek, F. and Rusek, J. (1994). Activity of digestive enzymes in 7 species of Collembola (Insecta, Entognatha). *Pedobiologia*, **38**, 400–6.
- Usher, M.B. (1969). Some properties of the aggregation of soil arthropods: Collembola. *Journal of Animal Ecology*, **38**, 607–22.
- Usher, M.B. (1970). Seasonal and vertical distribution of a population of soil arthropods: Collembola. *Pedobiologia*, **10**, 224–36.
- Usher, M.B. (1983). Species diversity: a comment on a paper by W.B. Yapp. *Field Studies*, **5**, 825–32.
- Usher, M.B. (1985). Population and community dynamics in the soil ecosystem. In *Ecological interactions in soil: plants, microbes and animals* (eds. A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher) pp. 243–65. Blackwell, Oxford.

- Usher, M.B. and Balogun, R.A. (1966). A defence mechanism in *Onychiurus* (Collembola, Onychiuridae). *Entomologist's Monthly Magazine*, **102**, 237–8.
- Usher, M.B. and Booth, R.G. (1984). Arthropod communities in a maritime Antarctic moss-turf habitat: three dimensional distribution of mites and Collembola. *Journal of Animal Ecology*, **53**, 427–41.
- Usher, M.B. and Booth, R.G. (1986). Arthropod communities in a maritime moss-turf habitat: multiple scales of pattern in the mites and Collembola. *Journal of Animal Ecology*, **55**, 155–70.
- Usher, M.B. and Bowring, M.F.B. (1984). Laboratory studies of predation by the Antarctic mite *Gamasellus racovitzai* (Acarina; Mesostigmata). *Oecologia*, **62**, 245–9.
- Usher, M.B. and Edwards, M. (1984). The terrestrial arthropods of the grass sward of Lynch island, a specially protected area in Antarctica. *Oecologia*, **63**, 143–4.
- Usher, M.B. and Hider, M. (1975). Studies on populations of *Folsomia candida* (Insecta: Collembola): causes of aggregations. *Pedobiologia*, **15**, 276–83.
- Usher, M.B. and Stoneman, C.F. (1977). *Folsomia candida*: an ideal organism for population studies in the laboratory. *Journal of Biological Education*, **11**, 83–90.
- Usher, M.B., Booth, R.G., and Sparkes, K.E. (1982). A review of progress in understanding the organisation of communities of soil arthropods. *Pedobiologia*, **23**, 126–44.
- Usher, M.B., Block, W., and Jumeau, P.J.A.M. (1989). Predation by arthropods in an Antarctic terrestrial community. In *Proceedings of the British Antarctic Survey Special Topic Award Scheme Symposium 1988*, pp. 117–22. British Antarctic Survey, Cambridge.
- Uvarov, A.V. (1994). Succession dynamics of Collembola in the course of decomposition of clover remains in soil. *Acta Zoologica Fennica*, **195**, 132–4.
- Van Amelsvoort, P.A.M. and Usher, M.B. (1989a). Egg production related to food type quality in *Folsomia candida* (Collembola: Isotomidae): effects on life history strategies. *Pedobiologia*, **33**, 61–6.
- Van Amelsvoort, P.A.M. and Usher, M.B. (1989b). A method for assessing the palatability of senesced leaf litter using *Folsomia candida* (Collembola, Isotomidae). *Pedobiologia*, **33**, 193–8.
- Van Amelsvoort, P.A.M., Van Dongen, M., and Van der Werff, P.A. (1988). The impact of Collembola on humification and mineralization of soil organic matter. *Pedobiologia*, **31**, 103–11.
- Van de Bund, C.F. (1972). Enkele waarnemingen aan *Laseoseius fimetorum* Karg, 1971 in een gezelschap van mijten, springstaarten en nematoden de wortels van witte klaver. *Entomologische Berichten*, **32**, 6–12.
- Van der Woude, H.A. (1987). Seasonal changes in cold hardiness of temperate Collembola. *Oikos*, **50**, 231–8.
- Van der Woude, H.A. and Joosse, E.N.G. (1988). The seasonality of respiration in two temperate Collembola as related to starvation, temperature and photoperiod. *Comparative Biochemistry and Physiology*, **91A**, 147–51.
- Van der Woude, H.A. and Verhoef, H.A. (1986). A comparative study of winter survival in two temperate Collembola. *Ecological Entomology*, **11**, 333–40.
- Van der Woude, H.A. and Verhoef, H.A. (1988). Reproductive diapause and cold hardiness in temperate Collembola *Orchesella cincta* and *Tomocerius minor*. *Journal of Insect Physiology*, **34**, 387–92.
- Vane-Wright, R.I., Humphries, C.J., and Williams, P.H. (1991). What to protect? – Systematics and the agony of choice. *Biological Conservation*, **55**, 235–54.
- Van Gestel, C.A.M. and Van Straalen, N.M. (1994). Ecotoxicological test systems for terrestrial invertebrates. In *Ecotoxicology of soil organisms* (eds. M.H. Donker, H. Eijssackers, and F. Heimbach), pp. 205–28. Lewis, Boca Raton.
- Vannier, G. (1971). Importance du point d'hygroscopie maximale dans une analyse factorielle du biotope des Collembolles. *Revue d'Écologie et de Biologie du Sol*, **8**, 81–9.
- Vannier, G. (1972). Estimation de la surface corporelle d'évaporation d'un Insecte aptérygote: *Allacma fusca* (L.), Collembole Symphyléone. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **274**, 258–61.
- Vannier, G. (1973a). Régulation du flux d'évaporation corporelle chez un Insecte Collembole vivant dans une atmosphère totalement desséchée. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **277**, 85–8.
- Vannier, G. (1973b). Étude de la transpiration chez un Insecte Collembole au cours de son exuviation. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **277**, 2231–4.
- Vannier, G. (1973c). Relations dimensionnellement homogènes entre la taille, la surface et le poids des individus de l'espèce *Allacma fusca* (L.), Insecte, Collembole. *Revue d'Écologie et de Biologie du Sol*, **10**, 559–73.
- Vannier, G. (1974a). Calcul de la résistance cuticulaire à la diffusion de vapeur d'eau chez un insecte Collembole. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **278**, 625–8.

- Vannier, G. (1974b). Variations du flux d'évaporation corporelle et de la résistance cuticulaire chez *Tetrodontophora bielanensis* (Waga), Insecte Collembole, vivant dans une atmosphère à régime hygrométrique variable. *Revue d'Écologie et de Biologie du Sol*, **11**, 201–11.
- Vannier, G. (1975a). Étude *in situ* du retour des microarthropodes sur des fractions de sol de granulométrie différente. *Bulletin d'Ecologie*, **6**, 87–98.
- Vannier, G. (1975b). Étude de la rétention hydrique chez l'insecte Collembole *Tetrodontophora bielanensis*. *Pedobiologia*, **15**, 68–80.
- Vannier, G. (1976). Évolution de l'équation linéaire entre poids frais et poids secs corporels dans une même population entomologique pendant une période de forte évaporation. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris*, **282**, 909–12.
- Vannier, G. (1977a). Water relationships in two species of Tomoceridae (Insecta, Collembola), a cave dwelling species and a top soil layer species. *Revue d'Écologie et de Biologie du Sol*, **14**, 31–5.
- Vannier, G. (1977b). Relations hydriques chez deux espèces de Tomoceridae (Insectes Collembolés) peuplant des niveaux écologiques séparés. *Bulletin de la Société Zoologique de France*, **102**, 63–79.
- Vannier, G. (1978a). La résistance à la desiccation chez les premiers arthropodes terrestres. *Bulletin de la Société Ecophysiologie*, **3**, 13–42.
- Vannier, G. (1978b). Étude expérimentale de l'effet immédiat du feu de litière sur les microarthropodes d'un sol forestier. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 3, Écologie Générale*, **42**, 51–63.
- Vannier, G. (1979a). Modification du flux d'évaporation corporelle sous l'effet d'une variation croissante de la température chez le collembole *Tomocerus minor*. *Bulletin de la Société Ecophysiologie*, **4**, 101–4.
- Vannier, G. (1979b). Relations trophiques entre la microfaune et la microflore du sol; aspects qualitatifs et quantitatifs. *Bollettino di Zoologia*, **46**, 343–61.
- Vannier, G. (1983). The importance of ecophysiology for both biotic and abiotic studies of the soil. In *New trends in soil biology* (ed. P. Lebrun, H.M. André, A. de Mets, C. Grégoire-Wibo, and G. Wauthy), pp. 289–314. Dieu-Brichart, Ottignies-Louvain-la-Neuve.
- Vannier, G. (1985). Modes d'exploitation et de partage des ressources alimentaires dans le système saprophage par les microarthropodes du sol. *Bulletin d'Ecologie*, **16**, 19–34.
- Vannier, G. (1987a). The porosphere as an ecological medium emphasized in Professor Ghilarov's work on soil animal adaptations. *Biology and Fertility of Soils*, **3**, 39–44.
- Vannier, G. (1987b). Mesure de la thermotorpeur chez les insectes. *Bulletin de la Société Ecophysiologie*, **12**, 165–86.
- Vannier, G. (1994). The thermobiological limits of some freezing intolerant insects: the supercooling and thermostupor points. *Acta Oecologia*, **15**, 31–42.
- Vannier, G. and Kilbertus, G. (1984). Mode de colonisation d'une bûche de bois mort par deux espèces d'insectes saprophages. *Revue d'Écologie et de Biologie du Sol*, **21**, 329–46.
- Vannier, G. and Massoud, Z. (1967). Productions ciréuses chez les Collembolés Neelidae. *Revue d'Écologie et de Biologie du Sol*, **4**, 123–30.
- Vannier, G. and Najt, J. (1991). Étude écophysiologique de collembole mélanésien *Caledonimeria mirabilis*: transpiration, thermotorpeur, cryorésistance. *Revue d'Écologie et de Biologie du Sol*, **28**, 175–87.
- Vannier, G. and Thibaud, J.M. (1971). Relation entre l'activité motrice d'une espèce de Collembolés cavernicoles et les variations de température dans son biotope. *Revue d'Écologie et de Biologie du Sol*, **8**, 261–86.
- Vannier, G. and Thibaud, J.M. (1978). Réduction ou perte totale de la capacité de régulation hydrique chez les espèces de Collembolés cavernicoles appartenant à la famille Tomoceridae. *Bulletin de la Société Ecophysiologie*, **3**, 124–6.
- Vannier, G. and Thibaud, J.M. (1984). Conséquences de la vie cavernicole sur l'écophysiologie et la biologie de l'insecte Collembole *Tomocerus catalanus* Denis. *Mémoires de Biospéologie*, **11**, 221–31.
- Vannier, G. and Verdier, B. (1981). Critères ecophysiologiques (transpiration, respiration) permettant de séparer une espèce souterraine d'une espèce de surface chez les Insectes Collembolés. *Revue d'Écologie et de Biologie du Sol*, **18**, 531–49.
- Vannier, G. and Verhoef, H.A. (1978). Effect of starvation on transpiration and water content in the populations of two co-existing Collembola species. *Comparative Biochemistry and Physiology*, **60A**, 483–9.
- Van Straalen, N.M. (1983). Demographic analysis of soil arthropod populations: a comparison of methods. *Pedobiologia*, **25**, 19–26.
- Van Straalen, N.M. (1985a). Comparative demography of forest floor Collembola populations. *Oikos*, **45**, 253–65.
- Van Straalen, N.M. (1985b). Size-specific mortality patterns in two species of forest floor Collembola. *Oecologia*, **67**, 220–3.

- Van Straalen, N.M. (1987). Turnover of accumulating substances in populations with weight-structure. *Ecological Modelling*, **36**, 195–209.
- Van Straalen, N.M. (1989). Production and biomass turnover in two populations of forest floor Collembola. *Netherlands Journal of Zoology*, **39**, 156–68.
- Van Straalen, N.M. (1993a). Soil and sediment quality criteria derived from invertebrate toxicity data. In *Ecotoxicology of metals in invertebrates* (ed. R. Dallinger and P.S. Rainbow), pp. 427–41. Lewis, Chelsea, USA.
- Van Straalen, N.M. (1993b). An ecotoxicologist in politics. *Oikos*, **66**, 142–3.
- Van Straalen, N.M. (1994a). Adaptive significance of temperature responses in Collembola. *Acta Zoologica Fennica*, **195**, 135–42.
- Van Straalen, N.M. (1994b). Biodiversity of ecotoxicological responses in animals. *Netherlands Journal of Zoology*, **44**, 112–29.
- Van Straalen, N.M. (in press). Community structure of soil arthropods as a bioindicator of soil health. In *Bioindicators of soil health* (ed. C.E. Pankhurst, B.M. Doube, and V.V.S.R. Gupta). CAB International Wallingford.
- Van Straalen, N.M. and De Goede, R.G.M. (1987). Productivity as a population performance index in life-cycle toxicity tests. *Water Science and Technology*, **19**, 13–20.
- Van Straalen, N.M. and Denneman, C.A.J. (1989). Ecotoxicological evaluation of soil quality criteria. *Ecotoxicology and Environmental Safety*, **18**, 241–51.
- Van Straalen, N.M. and Ernst, W.H.O. (1991). Metal biomagnification may endanger species in critical pathways. *Oikos*, **62**, 255–6.
- Van Straalen, N.M. and Joosse, E.N.G. (1985). Temperature responses of egg production and egg development in two species of Collembola. *Pedobiologia*, **28**, 265–73.
- Van Straalen, N.M. and Van Diepen, A.M.F. (1995). Evaluation of the Arrhenius activation energy in soil arthropods. *Proceedings of Experimental and Applied Entomology (Netherlands Entomological Society)*, **6**, 113–18.
- Van Straalen, N.M. and Van Gestel, C.A.M. (1993). Soil invertebrates and microorganisms. In *Handbook of ecotoxicology*, Vol. 1 (ed. P. Calow), pp. 251–77. Blackwell, Oxford.
- Van Straalen, N.M. and Van Meerendonk, J.H. (1987). Biological half-lives of lead in *Orchesella cincta* (L.) (Collembola). *Bulletin of Environmental Contamination and Toxicology*, **38**, 213–19.
- Van Straalen, N.M. and Van Wensem, J. (1986). Heavy metal content of forest litter arthropods as related to body-size and trophic level. *Environmental Pollution*, **42A**, 209–21.
- Van Straalen, N.M., Burghouts, T.B.A., and Doornhof, M.J. (1985). Dynamics of heavy metals in populations of Collembola in a contaminated pine forest soil. *Proceedings of the International Conference on Heavy Metals in the Environment, Athens 1985*, Vol. 1, pp. 613–15. CEP Consultants, Edinburgh.
- Van Straalen, N.M., Groot, G.M., and Zoomer, H.R. (1986). Adaptation of Collembola to heavy metal soil contamination. *Proceedings of the International Conference on Environmental Contamination, Amsterdam 1986*, pp. 16–20. CEP Consultants, Edinburgh.
- Van Straalen, N.M., Burghouts, T.B.A., Doornhof, M.J., Groot, G.M., Janssen, M.P.M., Joosse, E.N.G., Van Meerendonk, J.H., Theeuwes, J.P.J.J., Verhef, H.A., and Zoomer, H.R. (1987). Efficiency of lead and cadmium excretion in populations of *Orchesella cincta* (Collembola) from various contaminated forest soils. *Journal of Applied Ecology*, **24**, 953–68.
- Van Straalen, N.M., Kraak, M.H.S., and Denneman, C.A.J. (1988). Soil microarthropods as indicators of soil acidification and forest decline in the Veluwe area, the Netherlands. *Pedobiologia*, **32**, 47–55.
- Van Straalen, N.M., Schobben, J.H.M., and De Goede, R.G.M. (1989). Population consequences of cadmium toxicity in soil microarthropods. *Ecotoxicology and Environmental Safety*, **17**, 190–204.
- Van Straalen, N.M., Verweij, R.A., and Van Brummelen, T.C. (1993). PAH concentrations in forest floor invertebrates in the vicinity of a blast furnace plant. In *Polycyclic aromatic compounds – synthesis, properties, analytical measurements, occurrence and biological effects* (ed. P. Garrigues and M. Lamotte), pp. 1001–6. Gordon and Breach, Yverdon, Switzerland.
- Van Straalen, N.M., Leeuwangh, P., and Stortelder, P.B.M. (1994). Progressing limits for soil ecotoxicological risk assessment. In *Ecotoxicology of soil organisms* (ed. M.H. Donker, H. Eijssackers, and F. Heimbach), pp. 397–409. Lewis, Boca Raton.
- Van Wensem, J., Vegter, J.J., and Van Straalen, N.M. (1994). Soil quality criteria derived from critical body concentrations of metals in soil invertebrates. *Applied Soil Ecology*, **1**, 185–91.
- Vasquez, M.M. and Palacios-Vargas, J.G. (1989). Une nouvelle espèce Mexicaine de *Axenylloides* et biogéographie de la lignée Xenyllodienne (Collembola, Odontellidae). *Revue Française d'Entomologie*, N.S., **11**, 37–41.
- Vasquez, M.M. and Palacios-Vargas, J.G. (1990). Nuevos registros y a spectos biogeograficos de los colem-bolos de la Sierra de la Laguna, B.C.S., Mexico. *Folia Entomológica Mexicana*, **78**, 5–22.

- Vegter, J.J. (1983). Food and habitat specialization in coexisting springtails (Collembola, Entomobryidae). *Pedobiologia*, **25**, 253–62.
- Vegter, J.J. (1987). Phenology and seasonal resource partitioning in forest floor Collembola. *Oikos*, **48**, 175–85.
- Vegter, J.J., De Bie, P., Dop, H. (1988a). Distributional ecology of forest floor Collembola (Entomobryidae) in the Netherlands. *Pedobiologia*, **31**, 65–73.
- Vegter, J.J., Jooisse, E.N.G., and Ernsting, G. (1988b). Community structure, distribution and population dynamics of Entomobryidae (Collembola). *Journal of Animal Ecology*, **57**, 971–81.
- Verdier, B. and Vannier, G. (1984). Modifications de la consommation d'oxygène chez les arthropodes terrestres à respiration cutanée soumis à différents déficits hygrométriques de l'air. *Compte Rendu Hebdomadaire des Séances de l'Académie des Sciences, Paris, Série III*, **299**, 563–6.
- Verhoef, H.A. (1981). Water balance in Collembola and its relation to habitat selection, water content, hemolymph osmotic pressure and transpiration during an instar. *Journal of Insect Physiology*, **27**, 755–60.
- Verhoef, H.A. (1984). Releaser and primer pheromones in Collembola. *Journal of Insect Physiology*, **30**, 665–70.
- Verhoef, H.A. (1995). Animal ecophysiology: cornerstone for soil ecosystem studies as exemplified by studies on arthropods. *Acta Zoologica Fennica*, **196**, 176–82.
- Verhoef, H.A. and De Goede, R.G.M. (1985). Effects of collembolan grazing on nitrogen dynamics in a coniferous forest. In *Ecological interactions in soil: plants, microbes and animals* (ed. A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher) pp. 367–76. Blackwell, Oxford.
- Verhoef, H.A. and Li, K.W. (1983). Physiological adaptations to the effects of dry summer periods in Collembola. In *New trends in soil biology* (ed. P. Lebrun, H.M. André, A. de Mets, C. Gregoire-Wibo, and G. Wauthy), pp. 345–56. Dieu-Brichart, Ottignies-Louvain-la-Neuve.
- Verhoef, H.A. and Nagelkerke, C.J. (1977). Formation and ecological significance of aggregations in Collembola. An experimental study. *Oecologia*, **31**, 215–26.
- Verhoef, H.A. and Prast, J.E. (1989). Effects of dehydration on osmotic and ionic regulation in *Orchesella cincta* (L.) and *Tomocerus minor* (Lubbock) (Collembola) and the role of the coelomoduct kidneys. *Comparative Biochemistry and Physiology*, **93A**, 691–4.
- Verhoef, H.A. and Van Selm, A.J. (1983). Distribution and population dynamics of Collembola in relation to soil moisture. *Holarctic Ecology*, **6**, 387–94.
- Verhoef, H.A. and Witteveen, J. (1980). Water balance in Collembola and its relation to habitat selection, cuticular water loss and water uptake. *Journal of Insect Physiology*, **26**, 201–8.
- Verhoef, H.A., Nagelkerke, C.J., and Jooisse, E.N.G. (1977a). Aggregation pheromones in Collembola (Apterygota); a biotic cause of aggregation. *Revue d'Écologie et de Biologie du Sol*, **14**, 2105.
- Verhoef, H.A., Nagelkerke, C.J., and Jooisse, E.N.G. (1977b). Aggregation pheromones in Collembola. *Journal of Insect Physiology*, **23**, 1009–13.
- Verhoef, H.A., Bosman, C., Bierenbroodspot, A., and Boer, H.H. (1979). Ultrastructure and function of the labial nephridia and the rectum of *Orchesella cincta* (L.) (Collembola). *Cell and Tissue Research*, **198**, 237–46.
- Verhoef, H.A., Witteveen, J., Van der Woude, H.A., and Jooisse, E.N.G. (1983). Morphology and function of the ventral groove of Collembola. *Pedobiologia*, **25**, 3–9.
- Verhoef, H.A., Prast, J.E., and Verweij, R.A. (1988). Relative importance of fungi and algae in the diet and nitrogen nutrition of *Orchesella cincta* (L.) and *Tomocerus minor* (Lubbock) (Collembola). *Functional Ecology*, **2**, 195–201.
- Verhoef, H.A., H.A., Dorel, F.G., and Zoomer, H.R. (1989). Effects of nitrogen deposition on animal-mediated nitrogen mobilization in coniferous litter. *Biology and Fertility of Soils*, **8**, 255–9.
- Vilkamaa, P. (1988a). Lists of the insect types in the Zoological Museum, University of Helsinki. 6. Collembola. *Acta Entomologica Fennica*, **52**, 1–8.
- Vilkamaa, P. (1988b). *Proisotoma* (*Proisotoma*) *oirota* sp.n. (Collembola, Isotomidae) from Western Siberia. *Annales Entomologici Fennici*, **54**, 163–7.
- Vilkamaa, P. (ed) (1994). VIII International Colloquium on Apterygota, Helsinki, Finland. *Acta Zoologica Fennica*, **195**, 1–156.
- Vilkamaa, P. and Huhta, V. (1986). Effects of fertilization and pH on communities of Collembola in pine forest soil. *Acta Zoologica Fennica*, **23**, 167–74.
- Villalobos, F.J. (1989). Los Collembola Poduromorpha (Apterygota: Insecta) y la sucesión secundaria del bosque mesófilo de montaña. *Biotam, VAT. Tamaulipas, México*, **1**, 45–52.
- Villalobos, F.J. (1990). Estudio preliminar sobre la abundancia y diversidad de los Collembola (Apterygota) de un bosque tropical del noreste de México. *Folia Entomológica Mexicana*, **80**, 5–29.

- Visser, S. (1985). Role of the soil invertebrates in determining the composition of soil microbial communities. In *Ecological interactions in soil: plants, microbes and animals* (ed. A.H. Fitter, D. Atkinson, D.J. Read, and M.B. Usher) pp. 297–317. Blackwell, Oxford.
- Visser, S. and Whittaker, J.B. (1977). Feeding preferences for certain litter fungi by *Onychiurus subtenuis* (Collembola). *Oikos*, **29**, 320–5.
- Visser, S., Whittaker, J.B., and Parkinson, D. (1981). Effects of collembolan grazing on nutrient release and respiration of a leaf litter inhabiting fungus. *Soil Biology and Biochemistry*, **13**, 215–18.
- Visser, S., Parkinson, D., and Hassall, M. (1987). Fungi associated with *Onychiurus subtenuis* (Collembola) in an aspen woodland. *Canadian Journal of Botany*, **65**, 635–42.
- Von Allmen, H. and Zettel, J. (1982). Populationsbiologische Untersuchungen zur Art *Entomobrya nivalis* (Collembola). *Revue Suisse de Zoologie*, **89**, 919–26.
- Von Allmen, H. and Zettel, J. (1983). Embryonic development and postembryonic growth in a population of *Entomobrya nivalis* (Collembola). *Revue d'Écologie et de Biologie du Sol*, **20**, 77–86.
- Von Allmen, H. and Zettel, J. (1984). Beitrag zur Kälteresistenz von *Entomobrya nivalis* (Collembola) in dem Schweizer Voralpen. *Zoologische Jahrbücher für Systematik*, **111**, 231–44.
- Wägele, J.W. (1994). Review of the methodological problems of 'computer cladistics' exemplified with a case study on isopod phylogeny (Crustacea: Isopoda). *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **32**, 77–81.
- Wägele, J.W. and Wetzel, R. (1994). Nucleic acid sequence data are not *per se* reliable for inference of phylogenies. *Journal of Natural History*, **28**, 749–61.
- Wahlgren, E.S. (1901). Über einige neue Collembola formen aus dem südwestlichen Patagonien. *Entomologisk Tidskrift*, **21**, 265–70.
- Waldorf, E.S. (1971a). The reproductive biology of *Sinella curviseta* (Collembola: Entomobryidae) in laboratory culture. *Revue d'Écologie et de Biologie du Sol*, **8**, 451–63.
- Waldorf, E.S. (1971b). Selective egg cannibalism in *Sinella curviseta* (Collembola: Entomobryidae). *Ecology*, **52**, 673–5.
- Waldorf, E.S. (1971c). Oviposition inhibition in *Sinella curviseta*. *Transactions of the American Microscopical Society*, **90**, 314–25.
- Waldorf, E.S. (1974a). Notes on *Sminthurus fuscus* (L.) and its phoretic Acari. *Revue d'Écologie et de Biologie du Sol*, **11**, 363–5.
- Waldorf, E.S. (1974b). Sex pheromone in the springtail *Sinella curviseta*. *Environmental Entomology*, **3**, 916–18.
- Walker, C.H., Hopkin, S.P., Sibly, R.M., and Peakall, D.B. (1996). *Principles of ecotoxicology*. Taylor and Francis, London.
- Wallace, M.M.H. (1973). The taxonomy and distribution of *Sminthurus viridis* and related species (Collembola: Sminthuridae) in Western Europe and Morocco. *Revue d'Écologie et de Biologie du Sol*, **10**, 211–24.
- Wallace, M.M.H. (1974). An attempt to extend the biological control of *Sminthurus viridis* (Collembola) to new areas of Australia by introducing a predatory mite, *Neomolgus capillatus* (Bdellidae). *Australian Journal of Zoology*, **22**, 519–29.
- Wallace, M.M.H. and Mahon, J.A. (1971). The ecology of *Sminthurus viridis* (Collembola). III. The influence of climate and land use on its distribution and that of an important predator, *Bdellodes lapidaria* (Acari: Bdellidae). *Australian Journal of Zoology*, **19**, 177–88.
- Walsh, M.I. and Bolger, T. (1990). Effects of diet on the growth and reproduction of some Collembola in laboratory cultures. *Pedobiologia*, **34**, 161–71.
- Walsh, M.I. and Bolger, T. (1993). Effects of diet on the interactions between *Hypogastrura denticulata* Bagnall and *Onychiurus furcifer* Börner in laboratory cultures. *European Journal of Soil Biology*, **29**, 155–60.
- Walter, D.E. (1987). Trophic behaviour of 'mycophagous' microarthropods. *Ecology*, **68**, 226–9.
- Walters, M.C. (1968). A study of *Sminthurus viridis* (L.) (Collembola) in Western Cape Province. *Entomology Memoirs, Pretoria*, **16**, 1–98.
- Waltz, R.D. (1990). Order Collembola. In *Systematics of the North American insects and arachnids: status and needs* (ed. M. Kosztarab and C.W. Schaefer), pp. 33–5. Virginia Agricultural Experiment Station, Blacksburg, Virginia.
- Waltz, R.D. and Hart, J.W. (1985). New synonymy in *Hypogastrura* (Collembola: Hypogastruridae). *Great Lakes Entomologist*, **18**, 159–60.
- Waltz, R.D. and Hart, J.W. (1987). Epitoky in *Hypogastrura* (*Cyclograna*) *horrida* Yosii, 1960 (Hexapoda: Collembola: Hypogastruridae). *Proceedings of the Indiana Academy of Sciences*, **95**, 275–6.
- Waltz, R.D. and Hart, J.W. (1995a). Cyclomorphosis in *Isotoma* (*Desoria*) *albella* (Collembola: Isotomidae). *Entomological News*, **106**, 113–14.

- Waltz, R.D. and Hart, J.W. (1995b). First report of males of *Tullbergia clavata* (Collembola: Onychiuridae). *Entomological News*, **106**, 115–16.
- Waltz, R.D. and Hart, J.W. (1995c). *Isotoma* (Desoria) *truncata*, a new species of Nearctic springtail (Collembola: Isotomidae). *Entomological News*, **106**, 117–22.
- Waltz, R.D. and McCafferty, W.P. (1979). Freshwater springtails (Hexapoda: Collembola) of North America. *Purdue University Agricultural and Experimental Station, Research Bulletin*, **960**, 1–32.
- Waltz, R.D. and McCafferty, W.P. (1984). Indication of mounting media information. *Entomological News*, **95**, 31–2.
- Wardle, D.A., Nicholson, K.S., and Yeates, G.W. (1993). Effect of weed management strategies on some soil-associated arthropods in maize and asparagus ecosystems. *Pedobiologia*, **37**, 257–69.
- Warnock, A.J., Fitter, A.H., and Usher, M.B. (1982). The influence of a springtail *Folsomia candida* (Insecta, Collembola) on the mycorrhizal association of leek *Allium porrum* and the vesicular-arbuscular mycorrhizal endophyte *Glomus fasciculatus*. *New Phytologist*, **90**, 285–92.
- Weidner, H. (1983). Collembola and Zygentoma imported to Hamburg. *Anzeiger für Schadlingskunde Pflanzenschutz Umweltschutz*, **56**, 105–7.
- Weiner, W.M. (1973). Une nouvelle espèce du genre *Neanurella* Cass. des Pieniny (Carpates, Pologne), Collembola, Neanuridae. *Bulletin de l'Académie Polonaise des Sciences, Série des Sciences Biologiques*, **21**, 531–4.
- Weiner, W.M. (1981). Collembola of the Pieniny National Park in Poland. *Acta Zoologica Cracoviensia*, **25**, 417–500.
- Weiner, W.M. (1983). *Karlstejnina rusekiana* sp.n. from Poland. *Revue d'Écologie et de Biologie du Sol*, **20**, 287–90.
- Weiner, W.M. (1986a). Onychiurinae Bagn. of North Korea: *Formosanochiurus* g.n., problems concerning the status of the genus *Onychiurus* Gerv. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 93–7. University of Siena, Siena.
- Weiner, W.M. (1986b). North Korean Collembola. IX. The genus *Willemia* Börner, 1901. *Acta Zoologica Cracoviensia*, **29**, 331–8.
- Weiner, W.M. (1988). New species from the genus *Micraphorura* Bagnall, 1949 (Onychiurinae, Collembola). *Acta Zoologica Cracoviensia*, **31**, 383–6.
- Weiner, W.M. (1989a). Morphological changes during postembryological development in *Ceratophysella armata* (Gisin, 1949). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 47–53. University of Siena, Siena.
- Weiner, W.M. (1989b). Onychiurinae (Onychiuridae, Collembola) of North Korea: species of the *Paronychiurus flavescens* (Kinoshita, 1916) group. *Acta Zoologica Cracoviensia*, **32**, 85–92.
- Weiner, W.M. (1990). Onychiuridae of Poland. New species of *Protaphorura* Absolon, 1901 from the Tatra Mts. *Acta Zoologica Cracoviensia*, **33**, 453–7.
- Weiner, W.M. (1991a). Une espèce nouvelle de *Mesaphorura* (Collembola, Tullbergiinae) de Pologne. *Revue d'Écologie et de Biologie du Sol*, **28**, 225–8.
- Weiner, W.M. (1991b). Collemboles Poduromorpha de Nouvelles-Calédonie. *Willemia neocaledonica* n.sp. (Hypogastruridae). *Bulletin de la Société Entomologique de France*, **96**, 93–5.
- Weiner, W.M. (1992). In memoriam Prof. Claude Delamare-Deboutteville (1918–1990). *Wiadomosci Entomologiczkie*, **11**, 179–82.
- Weiner, W.M. (1994). Onychiurinae Bagnall of North Korea: species with small postantennal organs (Collembola, Onychiuridae). *Bulletin de la Société Entomologique de France*, **99**, 31–40.
- Weiner, W.M. (1996). Generic revision of Onychiurinae (Collembola: Onychiuridae) with a cladistic analysis. *Annales de la Société Entomologique de France*, N.S., **32**, 163–200.
- Weiner, W.M. and Betsch, J.M. (1992). Collemboles Symphypléones de Corée du Nord. Le genre *Bothriovulsus* Richards, 1968 (Dicyrtomidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **14A**, 81–91.
- Weiner, W.M. and Fjellberg, A. (1994). Redescription and lectotype designation of *Hymenaphorura sibirica* (Tullberg, 1876) (Collembola: Onychiuridae). *Entomologica Scandinavica*, **25**, 415–17.
- Weiner, W.M. and Najt, J. (1985a). Collemboles de Corée du Nord. IV. Brachystomellinae, Frieseinae et Pseudachorutinae ad partem. *Acta Zoologica Cracoviensia*, **28**, 245–76.
- Weiner, W.M. and Najt, J. (1985b). North Korean Collembola. V. The genus *Granurida* Yosii, 1954. *Acta Zoologica Cracoviensia*, **28**, 277–82.
- Weiner, W.M. and Najt, J. (1991a). Collemboles Poduromorpha de Nouvelle-Calédonie. 6. Onychiuridae Tullbergiinae. *Mémoires du Muséum National d'Histoire Naturelle*, **149A**, 119–30.
- Weiner, W.M. and Najt, J. (1991b). Collembola Poduromorpha of South Africa. *Bonner Zoologische Beiträge*, **42**, 369–87.

- Weiner, W.M. and Najt, J. (1994). Une nouvelle espèce de *Tillieria* (Collembola, Tullbergiinae) de l'île King George. *Polskie Pismo Entomologiczne*, **63**, 17–21.
- Weiner, W.M. and Stomp, N. (1995). Redescription of *Protaphorura eichhorni* (Gisin, 1954) (Collembola, Onychiurinae). *Bulletin Société des Naturalistes Luxembourgeois*, **96**, 121–6.
- Weiner, W.M. and Thibaud, J.M. (1991). Un nouveau genre de Tullbergiinae (Collembola) des sables de la région parisienne. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4*, **13A**, 113–19.
- Wetton, M.N. (1987). Morphological variation in British *Folsomia quadrioculata* Tullberg (Collembola: Isotomidae): a multivariate study. *Systematic Entomology*, **12**, 257–70.
- Wetton, M.N. (1988). A morphometric analysis of mandibular teeth in *Folsomia* (Collembola, Isotomidae). *Zoological Journal of the Linnean Society*, **94**, 99–109.
- Whalley, P. (1995). Unfair to ancient fossil springtails! *Antenna*, **19**, 2–3.
- Whalley, P. and Jarzembowski, E.A. (1981). A new assessment of *Rhyniella*, the earliest known insect, from the Devonian of Rhynie, Scotland. *Nature*, **291**, 317.
- Whipps, J.M. (1993). Growth of the collembolan *Folsomia candida* on cultures of the mycoparasite *Coniothyrium minitans* and sclerotia of *Sclerotinia sclerotiorum*. *Mycological Research*, **97**, 1277–80.
- Whipps, J.M. and Budge, S.P. (1993). Transmission of the mycoparasite *Coniothyrium minitans* by a collembolan *Folsomia candida* (Collembola: Entomobryidae) and glasshouse sciarid *Bradysia* sp. (Diptera: Sciaridae). *Annals of Applied Biology*, **123**, 165–71.
- Whittaker, J.B. (1981). Feeding on *Onychiurus subtenuis* (Collembola) at snow melt in aspen litter in the Canadian Rocky Mountains. *Oikos*, **36**, 203–6.
- Whittemore, A.T. (1993). Species concepts: a reply to Ernst Mayr. *Taxon*, **42**, 573–83.
- Wibo, C. (1973). Étude de l'action d'un insecticide organophosphoré sur quelques populations de microarthropodes édaphiques. *Pedobiologia*, **13**, 150–63.
- Wiggins, E.A. and Curl, E.A. (1979). Interactions of Collembola and microflora of cotton rhizosphere. *Phytopathology*, **69**, 244–9.
- Wiggins, E.A., Curl, E.A., and Harper, J.D. (1979). Effects of soil fertility and cotton rhizosphere on populations of Collembola. *Pedobiologia*, **19**, 75–82.
- Wiles, J.A. and Frampton, G.K. (1996). A field bioassay approach to assess the toxicity of insecticide residues on soil to Collembola. *Pesticide Science*, **47**, 273–85.
- Willem, V. (1906). Un nouveau Collembole marin (*Anuridella marina*). *Mémoires de la Société Entomologique de Belgique*, **12**, 247–52.
- Williets, H.M., Thomson, A.R., and Morris, G.E.L. (1989). Laboratory studies on the selection of *Pythium ultimum*, a plant-pathogenic fungus by *Onychiurus auranticus* (Collembola). *Aspects of Applied Biology*, **22**, 373–8.
- Wilson, E.O. (1992). *The diversity of life*. Penguin, London.
- Wilson, J.M. (1982). A review of world Troglopedetini (Insecta, Collembola, Paronellidae) including an identification table and descriptions of new species. *Cave Science*, **9**, 210–26.
- Wilson, K., Gunn, A., and Cherrett, J.M. (1995). The application of a rhizotron to study the subterranean effects of pesticides. *Pedobiologia*, **39**, 132–43.
- Wise, K.A.J. (1967). Collembola (Springtails). In *Entomology of Antarctica*, Antarctic Research Series No. 10 (ed. J.L. Gressitt), pp. 123–48. American Geophysical Union, Washington.
- Wise, K.A.J. (1970a). Collembola of South Georgia. *Pacific Insects Monographs*, **23**, 183–208.
- Wise, K.A.J. (1970b). Collembola of Heard Island. *Pacific Insects Monographs*, **23**, 209–15.
- Wise, K.A.J. (1971). The Collembola of Antarctica. *Pacific Insects Monographs*, **25**, 57–74.
- Wise, K.A.J. (1977). A synonymic checklist of the Hexapoda of the New Zealand sub-region. The smaller orders. *Bulletin of the Auckland Institute Museum*, **11**, 1–176.
- Witalis, J. (1993). Differentiation of somatic cells in the adult testes of the collembolan *Tetrodontophora bielanensis* (Hexapoda). *Cytobios*, **75**, 37–48.
- Witteveen, J. (1988). the impact of the salinity of soil-water and food on the physiology, behaviour and ecology of salt-marsh Collembola. *Functional Ecology*, **2**, 49–55.
- Witteveen, J. and Joosse, E.N.G. (1982). Distribution and salt tolerance of springtails (Collembola) in salt marshes. *Netherlands Journal of Zoology*, **32**, 276.
- Witteveen, J. and Joosse, E.N.G. (1987). Growth, reproduction and mortality in marine littoral Collembola at different salinities. *Ecological Entomology*, **12**, 459–69.
- Witteveen, J. and Joosse, E.N.G. (1988). The effects of inundation on marine littoral Collembola. *Holarctic Ecology*, **11**, 1–7.
- Witteveen, J., Verhoef, H.A., and Letschert, J.P.W. (1987). Osmotic and ionic regulation in marine littoral Collembola. *Journal of Insect Physiology*, **33**, 59–66.
- Witteveen, J., Verhoef, H.A., and Huipen, T.E.A.M. (1988). Life history strategy and egg diapause in the intertidal collembolan *Anurida maritima*. *Ecological Entomology*, **13**, 443–51.

- Wolters, V. (1983). Ökologische Untersuchungen an Collembolen eines Buchenwald auf Kalk. *Pedobiologia*, **25**, 73–85.
- Wolters, V. (1985). Resource allocation in *Tomocerus flavescens* (Insecta, Collembola): a study with C14-labelled food. *Oecologia*, **65**, 229–35.
- Wolters, V. (1991). Biological processes in two beech forest soils treated with simulated acid rain: a laboratory experiment with *Isotoma tigrina* (Insecta, Collembola). *Soil Biology and Biochemistry*, **23**, 381–90.
- Womersley, H. (1932). Collembola from Krakatau. *Entomologist's Monthly Magazine*, **68**, 88.
- Womersley, H. (1933). A possible biological control of the clover springtail or Lucerne Flea (*Sminthurus viridis* L.) in Western Australia. *Journal for the Council for Scientific and Industrial Research, Melbourne*, **6**, 83–91.
- Womersley, H. (1934). Collembola (Springtails). *Victorian Naturalist*, **51**, 159–65.
- Wood, T.G. (1967a). Acari and Collembola of moorland soils from Yorkshire, England. I. Descriptions of the sites and their populations. *Oikos*, **18**, 102–17.
- Wood, T.G. (1967b). Acari and Collembola of moorland soils from Yorkshire, England. II. Vertical distribution in four grassland soils. *Oikos*, **18**, 137–40.
- Wood, T.G. (1967c). Acari and Collembola of moorland soils from Yorkshire, England. III. The microarthropod communities. *Oikos*, **18**, 277–92.
- Worland, M.R. and Block, W. (1986). Survival and water loss in some Antarctic arthropods. *Journal of Insect Physiology*, **32**, 579–84.
- World Conservation Monitoring Service (1992). *Global diversity: status of the Earth's living resources*. Chapman and Hall, London.
- Wotton, E. (1552). *De differentiis animalium libri decem*. Michael Vascosanus, Paris.
- Wright, E.P. and Haliday, A.H. (1857). Notes on a visit to Mitchelstown caves. *Natural History Review*, **4**, 231–41.
- Xué, L., Dallai, R., and Yin, W. (1994). Comparative tracheal structures of Apterygota. *Acta Zoologica Fennica*, **195**, 143–9.
- Yosii, R. (1956a). Monographie zur Höhlencollembolen Japans. *Contributions from the Biological Laboratory, Kyoto University*, **3**, 1–109.
- Yosii, R. (1956b). Höhlencollembolen Japans. II. *Japanese Journal of Zoology*, **11**, 609–27.
- Yosii, R. (1958). On some remarkable Collembola from Japan. *Acta Zoologica Cracoviensia*, **2**, 681–705.
- Yosii, R. (1961). Phylogenetische Bedeutung der Chaetotaxie bei den Collembolen. *Contributions from the Biological Laboratory, Kyoto University*, **12**, 1–37.
- Yosii, R. (1962). Studies on the collembolan genus *Hypogastrura*. II. Nearctic forms collected by Prof. F. Bonet. *Contributions from the Biological Laboratory, Kyoto University*, **13**, 1–25.
- Yosii, R. (1964). Some Collembola of the Tonga Islands. *Kontyu, Tokyo*, **32**, 9–17.
- Yosii, R. (1965). On some Collembola of Japan and adjacent countries. *Contributions from the Biological Laboratory, Kyoto University*, **19**, 1–71.
- Yosii, R. (1966a). On some Collembola of Afganistan, India and Ceylon, collected by the Kuphe Expedition, 1960. *Results of the Kyoto University Scientific Expedition to the Karakoram and Hindukush*, **8**, 333–405.
- Yosii, R. (1966b). Snow Collembola of the Siachen Glacier in Karakoram. *Results of the Kyoto University Scientific Expedition to the Karakoram and Hindukush*, **8**, 407–10.
- Yosii, R. (1966c). Results of the speleological survey in South Korea 1966. IV. Cave Collembola of South Korea. *Bulletin of the National Science Museum, Tokyo*, **9**, 541–61.
- Yosii, R. (1966d). Collembola of Himalaya. *Journal of the College of Arts and Science, Chiba University*, **4**, 461–531.
- Yosii, R. (1967a). Studies on the Collembolan Family Tomoceridae, with special reference to Japanese forms. *Contributions from the Biological Laboratory, Kyoto University*, **20**, 1–54.
- Yosii, R. (1967b). Some cave Collembola of Japan. *Bulletin of the Akiyoshida Science Museum*, **4**, 61–6.
- Yosii, R. (1969). *Dicyrtomina* and *Ptenothrix* (Insecta: Collembola) of the Solomon Islands. *Zoological Journal of the Linnean Society*, **48**, 217–36.
- Yosii, R. (1970). On some Collembola of Japan and adjacent countries. II. *Contributions from the Biological Laboratory, Kyoto University*, **23**, 1–32.
- Yosii, R. (1971a). Halophilous Collembola of Japan. *Publications of the Seto Marine Biological Laboratory*, **18**, 279–90.
- Yosii, R. (1971b). Collembola of Khumbu Himal. In 'Khumbu Himal' *Universitätsverlag Wagner*, **4**, 80–130.
- Yosii, R. (1976a). On some Neanurid Collembola of Southeast Asia. *Nature and Life in South East Asia*, **7**, 257–99.
- Yosii, R. (1976b). Structure and chaetotaxy of labrum as the taxonomic character of Collembola. *Revue d'Écologie et de Biologie du Sol*, **13**, 233–9.

- Yosii, R. (1977). Critical checklist of the Japanese species of Collembola. *Contributions from the Biological Laboratory, Kyoto University*, **25**, 141–70.
- Yoshii, R. (1980). Cyphoderid Collembola of Sabah. *Contributions from the Biological Laboratory, Kyoto University*, **26**, 1–16.
- * From 1980 onwards, Yosii changed the English spelling of his name to Yoshii.
- Yoshii, R. (1981). Paronellid Collembola of Borneo. *Entomological Reports from the Borneo Forest Research Centre*, **3**, 1–51.
- Yoshii, R. (1982). Studies on the collembolan genus *Callyntrura* and *Dicranocentroides*. *Entomological Reports from the Borneo Forest Research Centre*, **6**, 1–68.
- Yoshii, R. (1983). Studies on paronellid Collembola of East Asia. *Entomological Reports from the Borneo Forest Research Centre*, **7**, 1–28.
- Yoshii, R. (1987). Notes on some cyphoderid Collembola of Tropical Asia. *Contributions from the Biological Laboratory, Kyoto University*, **27**, 121–36.
- Yoshii, R. (1988). Paronellid Collembola from caves of Central and South America collected by P. Strinati. *Revue Suisse de Zoologie*, **95**, 449–59.
- Yoshii, R. (1989a). Finding of *Lepidosinella armata* Handschin from East Java. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 89–91. University of Siena, Siena.
- Yoshii, R. (1989b). On some Collembola of New Caledonia, with notes on the colour pattern of the species. *Contributions from the Biological Laboratory, Kyoto University*, **27**, 233–59.
- Yoshii, R. (1990). Report on the cryophilous Collembola collected by Dr. S. Kohshima. *Contributions from the Biological Laboratory, Kyoto University*, **27**, 523–33.
- Yoshii, R. (1991). On *Ceratophysella* and *Schaefferia*. *Annals of Speleological Institute of Japan*, **9**, 3–10.
- Yoshii, R. (1992a). Identity of some Japanese Collembola. *Acta Zoologica Asiae Orientalis*, **2**, 97–110.
- Yoshii, R. (1992b). Interim report of the taxonomic researches toward the collembolan family Cyphoderidae. *Contributions from the Biological Laboratory, Kyoto University*, **28**, 99–118.
- Yoshii, R. and Greenslade, P. (1993). New records and new species of paronellid and cyphoderid Collembola from the Indonesian region, mainly Sulawesi. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, **10**, 75–86.
- Yoshii, R. and Greenslade, P. (1994). Reconnaissance of some entomobryid Collembola of Australia. *Acta Zoologica Asiae Orientalis*, **3**, 1–22.
- Yosii, R. and Lee, C. (1963). On some Collembola of Korea with notes on the genus *Ptenothrix*. *Contributions from the Biological Laboratory, Kyoto University*, **15**, 1–37.
- Yoshii, R. and Suhardjono, Y.R. (1989). Notes on the collembolan fauna of Indonesia and its vicinities. I. Miscellaneous notes, with special reference to Seirini and Lepidocyrtini. *Acta Zoologica Asiae Orientalis*, **1**, 23–90.
- Yoshii, R. and Suhardjono, Y.R. (1992a). Notes on the collembolan fauna of Indonesia and its vicinities. II. Collembola of Irian Jaya and Maluku islands. *Acta Zoologica Asiae Orientalis*, **2**, 1–52.
- Yoshii, R. and Suhardjono, Y.R. (1992b). Notes on the collembolan fauna of Indonesia and its vicinities. III. Collembola of Timor Island. *Acta Zoologica Asiae Orientalis*, **2**, 75–96.
- Zeh, D.W., Zeh, J.A., and Smith, R.L. (1989). Ovipositors, amnions and eggshell architecture in the diversification of terrestrial arthropods. *Quarterly Reviews of Biology*, **64**, 147–68.
- Zerling, L. (1990). Zur Sukzession von Kleinarthropoden, insbesondere Collembolen, im Bodenbildungsprozeß auf einer landwirtschaftlich genutzten Braunkohlenkippe bei Leipzig. *Pedobiologia*, **34**, 315–35.
- Zettel, J. (1982a). Age dependence of cold hardiness in *Isotoma hiemalis* and some other springtails. *Cryo Letters*, **3**, 311.
- Zettel, J. (1982b). Dietary influence on the biology and metabolism of *Isotoma viridis* (Collembola). *Journal of Insect Physiology*, **28**, 453–8.
- Zettel, J. (1984a). The significance of temperature and barometric pressure changes for the snow surface activity of *Isotoma hiemalis* (Collembola). *Experientia*, **40**, 1369–72.
- Zettel, J. (1984b). Cold hardiness strategies and thermal hysteresis in Collembola. *Revue d'Écologie et de Biologie du Sol*, **21**, 189–203.
- Zettel, J. (1985). Die Cyclomorphose von *Isotoma hiemalis* (Collembola): Endogene Steuerung, phänologische und physiologische Aspekte. *Zoologische Jahrbücher für Systematik*, **112**, 383–404.
- Zettel, J. and Klinger, J. (1983). Influence of sewage sludge application on microarthropods (Collembola and mites) and nematodes in a sandy loam soil. In *The influence of sewage sludge application on physical and biological properties of soils* (ed. G. Catroux, P. L'Hermite, and E. Süß), pp. 167–9. Reider, Dordrecht.

- Zettel, J. and Von Allmen, H. (1982). Jahresverlauf der Kälteresistenz zweier Collembolen-Arten in der Berner Voralpen. *Revue Suisse de Zoologie*, **89**, 927–39.
- Zettel, J. and Zettel, U. (1986). Influence of the cyclomorphosis on the winter behaviour of *Isotoma hiemalis* (Collembola). In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 117–21. University of Siena, Siena.
- Zettel, J. and Zettel, U. (1989). Photoperiodic synchronization of the seasonal polymorphism with the seasons in *Isotoma hiemalis* (Collembola). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 449–55. University of Siena, Siena.
- Zettel, J. and Zettel, U. (1994a). Development, phenology and surface activity of *Ceratophysella sigillata* (Uzel) (Collembola: Hypogastruridae). *Acta Zoologica Fennica*, **195**, 150–3.
- Zettel, U. and Zettel, J. (1994b). Seasonal and reproductional polymorphism in *Ceratophysella sigillata* (Uzel) (Collembola: Hypogastruridae). *Acta Zoologica Fennica*, **195**, 154–6.
- Zettel, J. and Zettel, U. (1994c). Adaptations to the alpine environment in *Isotomurus alticola* (Collembola: Isotomidae) in the Swiss Alps. *Acta Oecologia*, **15**, 93–104.
- Zettel, J., Meier, P., Suter, E., and Von Allmen, H. (1989). Difference in cold hardness strategies and the presence of cryoprotectants in two subalpine springtails: *Isotoma hiemalis* and *Entomobrya nivalis*. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 429–36. University of Siena, Siena.
- Zhao, L. and Tamura, H. (1992). Two new species of isotomid Collembola from Mt. Wuyanling, East China. *Edaphologia*, **48**, 17–21.
- Zimdars, B. and Dunger, W. (1994). Synopses on Palaearctic Collembola. Part 1. Tullbergiinae Bagnall, 1935. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **68**, 1–71.
- Zinkler, D. (1983). Ecophysiological adaptations of litter-dwelling Collembola and tipulid larvae. In *New trends in soil biology* (ed. P. Lebrun, H.M. André, A. de Mets, C. Gregoire-Wibo, and G. Wauthy), pp. 335–43. Dieu-Brichart, Ottignies-Louvain-la-Neuve.
- Zinkler, D. and Rüssbeck, R. (1986). Ecophysiological adaptations of Collembola to low oxygen concentrations. In *Second International Seminar on Apterygota* (ed. R. Dallai), pp. 123–7. University of Siena, Siena.
- Zinkler, D. and Schroff, G. (1989). The energetics of a jumping springtail *Tomocerus flavescens* (Collembola). In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 443–8. University of Siena, Siena.
- Zinkler, D. and Wilking, K. (1989). Pigmentation of Collembola: an ecophysiological approach. In *Third International Seminar on Apterygota* (ed. R. Dallai), pp. 467–75. University of Siena, Siena.
- Zinkler, D., Götze, M., and Fabian, K. (1987). Cellulose digestion in 'primitive insects' (Apterygota) and oribatid mites. *Zoologisches Beiträge*, **30**, 17–28.

Subject index

References to figures are in **bold**, those for tables are in *italics*.

- abundance 4, 5, **170–2**
Actaletidae 27, **35**, 35, 211
aggregation 163–4, **163**
allozyme analysis 81
amber 23–4, **25**
antennae 22, 36, 38, 42, 47–8, 67–8, **67, 86, 87, 138**
ants, association of Collembola with 35, 126
Aristotle 8
Arthropleona 27, 202
atmobiote, *see* epedaphic
- bees, association of Collembola with 35
biogeography 42–5
biomass 5
blood 59, 101–2, **109**
Bourletiellinae 27, 41, **139**, 218
Brachystomellidae 27, 29–30, **29**, 202
brain 64, **66**
- Caputanurinae 27, 30, **31**, 204
carnivory, *see* diet
cave Collembola 180–2, **182**
cellulase 62
chaetotaxy 82–5, **84, 88**
chromosomes 34, 78–81, **79, 80**, 135–6
classification 2, 19–23, **20, 22**, 26–8, 27
claw **48**
Coenaletidae 27, 35, 211
cold hardiness 102–3
Collembola, derivation of name 2
colour 2–3, 31, 37, 82
commensalism 35
competition between Collembola 126–7
conservation 178–80
continental drift 43
coxa **48**
cuticle 51–7, **53, 54**
cyclomorphosis 153–6, **154, 155**, 155
Cyphoderidae 27, 35, 211
- decomposition 6, 127–9
defensive secretions, *see* pseudocelli
De Geer **9**, 9, 12
dens **48**
desiccation resistance 106–8, **108**
development 22, 142–53
 abnormal 150, **150, 151**
 of eggs 100, 142–9, **149**
- Dicyrtominae 27, 41–2, **41**, 219
diet
 assimilation efficiencies 113–14
 carnivory 3, 30, 51, 116–7
 composition 114–23
 fungus 3, 6, 47, 63, **115**, 117–23, **118, 119, 120, 121, 122, 122**
 preferences 116
digestive enzymes 62
digestive tract 60–4, **61**
dispersal 5, 43–4, 160–3, **161, 162**, 165–8
distribution maps 44–5
diversity 4
DNA, sequence analysis of 81
dominance patterns 5, **170**
- ecological indicators 173–8, **176**
ecomorphology 46–7
ecomorphosis 153–6, **154, 155**, 155
ecophysiology 98
ecotoxicology 183–201
eggs 134–5, 142, **143**
ejaculatory duct **137**
embryology 142–9, **144–8**
empodium **48**
entognathy 2, 50
Entomobryidae 27, 36, 212
Entomobryinae 27, 36, 212
Entomobryoidea 27, 29, 211
Entomobryomorpha, *see* Entomobryoidea
epedaphic 46
epitoky 153–6, **154, 155**, 155
euedaphic 46
evolution 25–6
excretion 64, 198–9, **199**
eyes 22, 69–70, **69**
- faeces 63
fat body 58
fecundity 141–2
feeding, *see* diet
femur **48**
fossils 23–4, **24**
freeze avoiding 101
freezing tolerance 102
Frieseinae 27, 30, 204
fungus, *see* diet
furca 2, **48**, 49–50, 70–2, **71, 72**

- gametes 134–5
 gas exchange 109–12
 genital plate 48
 global distribution 4
 granules, in midgut cells 63, **64**, 64, 198–9
 guilds 47
 Gulgastrurinae 27, 30, 203
 gut, *see* digestive tract
- habitat preferences 175–6, **176**
 hamula, *see* tenaculum
 hemiedaphic 46
 hermit crabs, association of Collembola with 35
 human infestation 3
 humidity **106**
 Hypogastruridae 27, **29**, 30, 203
 Hypogastrurinae 27, **29**, 30, 203
 hypopharynx 50, **49**, **50**
- Isotogastrurinae 27, 30, 204
 Isotomidae **ii**, 27, 36, **48**, **184**, 213
- jumping 70–2, **71**
- Katianninae 27, 42, **182**, 219
- labial nephridia **58**, 59–60
 labium 50, **49**, **50**
 labrum 50, **49**, **50**
 leg **48**
 life forms, *see* ecomorphology
 life histories 133–4, 152–3
 linea ventralis 49, **60**, **104**
 Linnaeus **10–11**, 12
 longevity 3
 Lubbock 14
- Mackenziellidae 27, 39, **40**, 218
 mandibles 50, **49**, **50**, **52**
 manubrium **48**
 mating behaviour 138–40, **139**, **140**
 maxilla 50–1, **49**, **50**, **51**, **52**, **83**
 Microfalculidae 27, 36, **37**, 216
 midgut 62–4, **63**
 migration, *see* dispersal
 Morulininae 27, 30–1, **32**, 205
 moulting 57, 105, 152
 mouthparts **49**, 50–1, 82
 mucro **48**, **91**
 muscles 59
- Neelidae 27, 38–9, **39**, 218
 Neelipleona 27, 29, 218
 nephridia, *see* labial nephridia
 nervous system 64, **65**, **66**
 neurosecretory system 64
- ocelli, *see* eyes
 Odontellidae 27, 33–4, 209
 olfaction 64–5
 Oncopoduridae 27, 37, 216
 Onychiuridae 27, 34, **92**, 209
 Onychiurinae 27, 34, **92**, 93–7, **93**, 95, **182**, 209
 oocytes, *see* eggs
 Orchesellinae **16**, 27, 36, **182**, 213
 osmoregulation 104, **109**
 oval organs 70
 ovaries 134–5
 oviposition 140–2, **141**
 oxygen consumption 112, **112**
- Pachytullbergiinae 27, 34, 210
 PAO, *see* post antennal organ
 parasites of Collembola 125–6
 Paronellidae 27, 37, **182**, 216
 parthenogenesis 156–7
 pests 3, 129–32
 pheromones 67, 126, 139, 164
 phylogeny, *see* classification
 pigmentation 56, **54**
 plastron 54, **55**, 111
 Poduridae 27, **29**, 34, 211
 Poduroidea 27, 28–9, 202
 Poduromorpha, *see* Poduroidea
 post antennal organ (PAO), **48**, 68–9 **68**
 predation on Collembola by
 beetles 46, 71, 123–5, **124**
 other invertebrates 123
 vertebrates 123
 pretarsus **48**
 proprioceptors 70
 Pseudachorutinae 27, **29**, 31, 207
 pseudocelli 34, 57–8, **57**, **68**, **93**
 pyloric region **62**, 62–3
- reproduction 134–42
 reproductive organs 134–5
 resistance 200–1
 retinaculum, *see* tenaculum
 risk assessment 189–92
- salivary glands 59
 Salmon 1, 6–7, 16
 salt balance 103–9
 sampling techniques 158–60
 scales 46, 56, **56**
 segmentation 47
- Neanuridae 27, **29**, 30–3, **31**, **32**, **33**, 204
 Neanurinae 27, 31, 205

- sense organs 64–70
setae 70, 82–5, **84**
sexual dimorphism 136–8, **138**
size 2, 3
Sminthuridae 27, 39–42, 218
Sminthuridinae 27, 42, **138**, 219
Sminthurinae **17**, 27, 42, 220
species
 concepts 74–5, **75**
 definition of 74, 85–93
 number of 3, 180
sperm 134, **135**
spermatophores 136, **137**, 139
Spinothercinae 27, 42, 110, 220
spring, *see* furca
standard test 186–9
starvation 113–14, **114**
Sturminae 27, 42, 220
subcoxa **48**
succession 168–73
supercooling point 100, **102**
'swarming' 3, 5
Symphypleona 27, 29, 218
systematic methods 76–85
- taste 65, 118
temperature 99–103, **99**, **101**, **102**, 149, **149**
tenaculum **48**, 49, 71–2
- tenant hairs 48
terminal web 62
termites, association of Collembola with 35, 126
testes 134
Tetrodontophorinae 27, 34, **92**, 210
thermal death point 100
thermobiological span 99–100
thermostupor point 100
tibiotarsus **48**
Tomoceridae **15**, 27, 38, **38**, **182**, 217
tracheae 59, 110, **110**
trochanter **48**
troglobites 181
troglophiles 181
trogloxenes 181
Tullbergiinae 27, 34, **92**, 210
- Uchidanurinae 27, 32–3, **33**, 208
urine 59
- ventral groove, *see* linea ventralis
ventral tube 2, 48–9, **48**, 103–5, **104**
vertical distribution 164, **165–7**, **169**
- water balance 103–9
wax, associated with cuticle 54

Systematic index

References to figures are in **bold**, those for tables are in *italics*. If the author and year of first description given after the genus and species name are in parentheses, then the species is now included in a different genus to that in which it was originally placed.

- Aackia karakoramensis* Yosii 1966 4
Actaletes neptuni Giard 1889 35
Adelphoderia regina Greenslade 1992 42
Allacma fusca (Linnaeus 1758) 9, **9**, **10**, **65**, 71, 105, **110**, 165
Allacma gallica (Carl 1899) 139, **140**
Allaphorura sp. 93
Americabrya matthewsi (Snider 1981) 123
Antarctophorus subpolaris (Salmon 1962) 4
Anurida sp. 31
Anurida forsslundi, see *Micranurida forsslundi*
Anurida granaria (Nicolet 1847) **166**
Anurida maritima (Guérin 1836) 4, 16, 22, **29**, 31, 54, **55**, 68, 103, 105, 107, 109, **109**, 134, **135**, 142, 143, 158
Anurida pygmaea see *Micranurida pygmaea*
Anuridella sp. 15, 31
Anuridella marina Willem 1906 54, **55**, 107
Anurophorus binoculatus, see *Pseudanurophorus binoculatus*
Anurophorus laricis Nicolet 1842 **166**
Anurophorus septentrionalis Palissa 1966 **165**
Anurophorus subpolaris, see *Antarctophorus subpolaris*
Archaphorura sp. **92**, 93
Archaphorura absoloni (Börner 1901) **165**
Archisotoma brucei (Carpenter 1907) **102**
Archisotoma megalops Bagnall 1939 4
Architomocerura sp. 90
Arrhopalites sp. 42, 117, 182
Arrhopalites pygmaeus (Wankel 1861) **182**
- Bessoniella procera* Deharveng and Thibaud 1989 **182**
Biscoia sudpolaris Salmon 1962 4
Bonetogastrura sp. 76
Bonetogastrura balazuci Delamare Deboutteville 1951 114
Bonetogastrura cavicola (Börner 1901) 69
Bourletiella sp. 160
Bourletiella hortensis (Fitch 1863) 41, 129, 130, 139, **139**, 170
Brachystomella sp. 15
Brachystomella parvula (Schäffer 1896) 29, **29**
- Caledonimeria mirabilis* Delamare Deboutteville and Massoud 1963 **33**
- Callyntrura chibai* Yoshii 1985 152
Campylothorax melanocephalus Mitra and Dallai 1980 37
Capitanurina nana, see *Leenurina nana*
Cephalotoma grandiceps, see *Metisotoma grandiceps*
Ceratophysella armata (Nicolet 1842) 133–4, **154**
Ceratophysella longispina (Tullberg 1876) 5
Ceratophysella sigillata (Uzel 1891) 154–6, 155
Ceratophysella sp. 30
Ceratophysella tergilobata (Cassagnau 1954) **52**
Choreutinula inermis (Tullberg 1871) **165**
Cliforga alleghaniensis Wray 1952 **155**
Coenaletes caribaeus Bellinger 1985 35
Coenaletes vangoethemi (Jacquemart 1980) 35
Collophora sp. 42
Crossodonthina koreana Yosii and Lee 1963 28
Cryptopygus antarcticus Willem 1901 **ii**, 36, 58, 102–3, **102**, 111, 112, **112**, 113, 152
Cryptopygus bipunctatus (Axelson 1903) 84
Cryptopygus fasciatus (Carpenter 1912) 90
Cryptopygus sp. 160
Cyphoderus sp. 35
- Denisimeria longilobata* Massoud 1965 2
Desoria graeca, see *Isotoma graeca*
Desoria tigrina, see *Isotoma tigrina*
Deuterosminthurus bicinctus (Koch 1840) 85
Deuterosminthurus flavus (Gisin 1946) 85
Deutonura deficiens Deharveng 1979 **52**
Deutonura sp. 76
Dicyrtoma minuta, see *Dicyrtomina minuta*
Dicyrtomina minuta (Fabricius 1783) **166**
Dicyrtomina ornata (Nicolet 1841) **41**, 72, **72**, 136
Dimorphaphorura sp. 93
Disparrhopalites patrizii (Cassagnau and Delamare Deboutteville 1953) 45
- Entomobrya aino* (Matsumura and Uchida 1931) 149, 153
Entomobrya albocincta (Templeton 1835) **176**
Entomobrya dorsalis Uzel 1890 70–1
Entomobrya lanuginosa (Nicolet 1841) **176**
Entomobrya monopunctata Lee and Park 1984 159
Entomobrya nivalis (Linnaeus 1758) 4, 9, **11**, 90, 123, 149, 158, 168, 176, **176**
Entomobrya sp. 36, 56, 89, 160, 165, **166**

- Folsomia candida* Willem 1902 vi, 36, **49**, 50, 57, **91**, 103–4, 111, **111**, 116, 118, **118**, **119**, 120, 121, 122, 127, 131, 141, 156–7, 160, 184–9, **184**, 187, **188**, 189, **190**, **197**, 201
Folsomia fimetaria (Linnaeus 1758) **11**
Folsomia fimetarioides (Axelson 1903) 65, 193, **195**, 201
Folsomia litsteri Bagnall 1939 96
Folsomia manolachei Bagnall 1939 **76**
Folsomia nigromaculata Najt 1981 **155**
Folsomia octoculata Handschin 1925 **170**, **172**
Folsomia quadrioculata (Tullberg 1871) **6**, 163, **165**, **166**, 193, **195**
Folsomia sensibilis Kseneman 1936 **165**
Folsomia sexoculata (Tullberg 1871) **99**
Folsomia sp. 76, **77**
Folsomides angularis (Axelson 1905) 107
Folsomides arnoldi Suhardjono and Greenslade 1994 4
Folsomides sp. 85, 107
Folsomina onychiurina **170**
Friezea mirabilis (Tullberg 1871) 30, **165**, **166**, **167**
Friezea sp. 15, 30, 43, 117
- Gulgastrura reticulosa* Yosii 1966 3, 152
- Harlomillsia oculata* (Mills 1937) 37
Heteromurus nitidus (Templeton 1835) 36, 46, 71, **111**, 124, 126, 152
Heteromurus sp. 82
Heterosminthurus insignis (Reuter 1876) **176**
Hymenaphorura sp. 85, **92**, 93
Hymenaphorura subtenuis (Folsom 1917) 168, **169**
Hypogastrura assimilis (Krausbauer 1898) 192
Hypogastrura boldorii Denis 1931 153, **154**
Hypogastrura inermis, see *Choreutinula inermis*
Hypogastrura manubrialis (Tullberg 1869) **83**
Hypogastrura meridionalis Steiner 1955 5
Hypogastrura notha (MacNamara 1922) **83**
Hypogastrura oregonensis Yosii 1960 **83**
Hypogastrura pannosa (MacNamara 1922) **83**
Hypogastrura purpurescens (Lubbock 1867) **154**
Hypogastrura socialis (Uzel 1891) 5, 67, 68, 69, 160, **161**, **162**
Hypogastrura sp. 4, 28, **29**, 30
Hypogastrura tullbergi (Schäffer 1900) **83**
Hypogastrura vernalis (Carl 1901) **83**
Hypogastrura viatica (Tullberg 1872) 56, 109, **109**, 126
- Isotogastrura* sp. 3
Isotoma agrelli Delamare Deboutteville 1950 **51**
Isotoma anglicana Lubbock 1862 96
Isotoma carpenteri Börner 1909 **170**, **172**
Isotoma ekmani Fjellberg 1977 **51**
Isotoma graeca Najt 1981 **155**
Isotoma hiemalis Schött 1893 153, **165**
Isotoma notabilis Schäffer 1896 **51**, 156, 157, **165**, **166**, **167**, 178, **179**, 193, 200
Isotoma olivacea Tullberg 1871 **165**, **166**, 193, **194**, 201
Isotoma palliceps, see *Isotomurus palliceps*
Isotoma sensibilis, see *Pseudisotoma sensibilis*
Isotoma sp. **54**, 90, 125, 156
Isotoma tigrina (Nicolet 1842) **155**
Isotoma violacea Tullberg 1876 **99**, 165, 178
Isotoma viridis Bourlet 1839 **48**, **65**, **99**, 109, **109**, 125, 127, **155**, **165**, **166**, **197**, **198**
Isotomiella minor (Schäffer 1896) 65, 156, **165**, **166**, 193, **195**
Isotomurus palliceps (Uzel 1890) **63**, **69**
Isotomurus palustris (Müller 1776) 12, 36, 81, **151**, **197**
Isotomurus plumosus Bagnall 1940 **166**, **167**
- Janetschekbrya matthewsi*, see *Americabrya matthewsi*
- Kalaphorura burmeisteri* (Lubbock 1873) **66**
Kalaphorura sp. **92**, 93
Kalaphorura tuberculata (Moniez 1891) = junior synonym of *Kalaphorura burmeisteri*
Karlstejnina norvegica Fjellberg 1974 **165**
- Lathriopyga longiseta* (Caroli 1912) **79**, **80**, 81
Leenurina nana (Lee 1983) **31**
Lepidocyrtus cyaneus Tullberg 1871 **165**
Lepidocyrtus lanuginosus (Gmelin 1788) **166**
Lepidocyrtus lignorum (Fabricius 1781) 89, **165**
Lepidocyrtus sp. 25, 36, 161
Lepidosinella armata Handschin 1920 126
Lepidosira calolepis (Börner 1913) 162
Lobella sp. 15
- Mackenziella psocoides* Hammer 1953 39, **40**, 58
Mastigoceras camponoti Handschin 1924 48
Megalothorax incertus Börner 1903 96
Megalothorax minimus Willem 1900 **39**, 54, 156, **165**, **166**, **167**
Mesachorutes sp. 15
Mesaphorura clavata (Mills 1934) 157
Mesaphorura italica (Rusek 1971) 157, **165**
Mesaphorura krausbaueri Börner 1901 74, 152, 156, 157, **166**, **167**
Mesaphorura macrochaeta Rusek 1976 156, **165**
Mesaphorura sp. 15
Mesaphorura sylvatica (Rusek 1971) 156, **165**
Mesaphorura tenuisensillata Rusek 1974 **165**
Mesaphorura yosii (Rusek 1967) **165**, **170**, **172**
Mesira calolesis, see *Lepidosira calolepis*
Metisotoma grandiceps (Reuter 1891) 51, 117

- Micranurida forsslundi* Gisin 1949 **165**
Micranurida pygmaea Börner 1901 **165**
Micraphorura absoloni, see *Archaphorura absoloni*
Micraphorura sp. 93
Microfalcula delamarei Massoud and Betsch 1966 36, **37**
Monobella grassei (Denis 1923) 125
Morulina gilvipunctata (Uchida 1938) 2
Morulina pawlowskii Deharveng and Weiner 1984 **32**
Morulina sp. 30–1
Mucrella acuminata (Cassagnau 1952) **83**
Mucrella navicularis (Schött 1893) **83**
- Neanura grassei*, see *Monobella grassei*
Neanura mandarina Yosii 1956 **170**
Neanura muscorum (Templeton 1835) 31, **52**, 157, 158, **166**
Neelus minimus, see *Megalothorax minimus*
Nepalimeria dal Cassagnau 1984 59
- Odontella* sp. 15, 34
Oligaphorura sp. **92**, 93
Oncopodura sp. 37
Ongulonychiurus colpus Thibaud and Massoud 1986 **182**
Ongulonychiurus sp. 93
Onychiurus absoloni, see *Archaphorura absoloni*
Onychiurus ambulans (Linnaeus 1758) **11**
Onychiurus armatus, see *Protaphorura armata*
Onychiurus decemsetosus Yosii 1966 **170**, **172**
Onychiurus folsomi (Schäffer 1900) 163
Onychiurus imperfectus Denis 1938 157
Onychiurus sp. 91, **92**, 93, 94, **106**, 160
Onychiurus subtenuis, see *Hymenaphorura subtenuis*
Orchesella bifasciata Nicolet 1841 200
Orchesella cincta (Linnaeus 1758) **11**, **16**, 36, **58**, 100, 102, 104–5, 124–5, 126, 129, 133, 136, **137**, 140, 149, **149**, 152, 185, 189, **199**, 200
Orchesella flavescens (Bourlet 1839) 105, 165
Orchesella sp. 56, 81, 89, 103, 134, 160
Orchesella villosa (Geoffroy 1764) 13, **71**, 100, 123, 125, 199, 200
- Papirinus prodigiosus* Yosii 1954 156
Paralobella orousseti Cassagnau and Deharveng 1984 2, 31
Paratullbergia callipygos (Börner 1902) 156, **165**, **166**
Parisotoma notabilis, see *Isotoma notabilis*
Parisotoma octooculata (Willem 1901) **102**, 112
Paronychiurus denisi (Stach 1934) 89
Paronychiurus paxi (Stach 1936) = junior synonym of *Paronychiurus denisi*
- Paronychiurus* sp. **92**, 93
Podura ambulans, see *Onychiurus ambulans*
Podura aquatica Linnaeus 1758 4, 9, **11**, 12, **13**, 28, **29**, 34, **83**, 104, 105, 135, 158, 176, **176**
Podura arborea, see *Vertagopus arboreus*
Podura atra, see *Ptenothrix atra*
Podura cincta, see *Orchesella cincta*
Podura fimetaria, see *Folsomia fimetaria*
Podura fusca, see *Allacma fusca*
Podura nivalis, see *Entomobrya nivalis*
Podura plumbea, see *Pogonognathellus longicornis*
Podura viridis, see *Sminthurus viridis*
Pogonognathellus flavescens (Tullberg 1871) **50**, **53**, **56**, **60**, 62, 70, **111**, 112
Pogonognathellus longicornis (Müller 1776) **11**, **15**, 38, **38**, 72, 123, **166**
Probolaphorura sp. 93
Proctostephanus madeirensis Gama 1959 45
Proctostephanus sp. 50
Proisotoma filifera Denis 1931 163
Proisotoma minuta (Tullberg 1871) 141
Proisotoma oliveirae Deharveng 1984 156
Proisotoma roberti Fjellberg 1991 103
Proisotoma sp. 163
Proisotoma subarctica Gisin 1950 22, **150**
Protanura sp. 15
Protaphorura alborufescens (Vogler, 1895) 95
Protaphorura arctica (Tullberg 1876) 95
Protaphorura armata (Tullberg 1869) 64, 77, **78**, **93**, 95, 108, **108**, 120, 121, 125, 131, **165**, 189, 193, **194**, 200
Protaphorura aurantiaca (Ridley 1880) **78**, 94, 95, 120
Protaphorura bagnalli (Salmon 1959) 95
Protaphorura bicampata (Gisin 1956) 95
Protaphorura caledonica (Bagnall 1935) 95
Protaphorura campata (Gisin 1952) 94, 95
Protaphorura debilis (Moniez 1890) 95
Protaphorura evansi (Bagnall 1935) 95
Protaphorura fimata (Gisin 1952) 95, 108, 178
Protaphorura flavidula (Bagnall 1939) 95
Protaphorura furcifera (Börner 1901) 95
Protaphorura halophila (Bagnall 1937) 95
Protaphorura hortensis (Gisin 1949) 95, 157
Protaphorura humata (Gisin 1952) **78**, 94, 95
Protaphorura imminuta (Bagnall 1937) 95
Protaphorura lata (Gisin 1956) 58, 94, 95, 120
Protaphorura magnicornis (Bagnall 1937) 95
Protaphorura meridiata (Gisin 1952) 94, 95, 112
Protaphorura nemorata (Gisin 1952) 94, 95
Protaphorura octopunctata (Tullberg 1876) 95
Protaphorura pannonica (Haybach 1960) 94, 95
Protaphorura procampata (Gisin 1956) 94, 95, 96
Protaphorura prolata (Gisin 1956) 94, 95
Protaphorura pseudocellata (Naglitsch 1962) 95
Protaphorura pulvinata (Gisin 1954) 94, 95
Protaphorura quadriocellata (Gisin 1943) **78**, 95
Protaphorura s-vontoernei (Gisin 1957) 95

- Protaphorura* sp. 15, **57**, **67**, **68**, **92**, 93, 94, 95, 96
(for a discussion of possible synonymies of
Protaphorura species, see Section 5.4, p. 93)
- Protaphorura stachi* (Bagnall 1935) 95
- Protaphorura subaequalis* (Bagnall 1937) 95
- Protaphorura subarmata* (Gisin 1957) 94, 95
- Protaphorura sublata* (Gisin 1957) 94, 95
- Protaphorura subuliginata* (Gisin 1956) 94, 95
- Protaphorura thalassophila* (Bagnall 1937) 95
- Protaphorura tricampata* (Gisin 1956) 94, 95 96
- Protaphorura trinotata* (Gisin 1961) 94, 95
- Protaphorura tullbergi* (Bagnall 1935) 95
- Protaphorura uliginata* (Gisin 1952) 94, 95
- Protaphorura waterstoni* (Bagnall 1937) 95
- Protaphorura yolandae* (Izarra 1971) 157
- Protentomobrya walkerii* (Folsom 1937) 25
- Pseudachorutes* sp. **22**, 31
- Pseudanurophorus binoculatus* Kseneman 1934
165
- Pseudisotoma sensibilis* (Tullberg 1876) 108, **108**,
163, **163**, **170**, **172**
- Pseudosinella decipiens* Denis 1924 3
- Pseudosinella hirsuta* (Delamare Deboutteville
1949) 181
- Pseudosinella impediens* (Gisin and Gama 1969)
152
- Pseudosinella* sp. 36, 96, 182
- Pseudosinella terricola* Gisin 1967 **115**
- Ptenothrix atra* (Linnaeus 1758) **10**, 54
- Rambutanura yoshiiana* Deharveng 1988 59
- Rhyniella praecursor* Hirst and Maulik 1926 viii,
23, **24**, 26
- Salina celebensis* (Schäffer 1898) 161
- Salina* sp. 37
- Schaefferia* sp. 76
- Schaefferia willemi* (Bonet 1930) **166**
- Seira domestica* (Nicolet 1841) 108
- Seira* sp. 25, 160
- Sinella coeca* (Schött 1896) **61**, 116, 126
- Sinella curviseta* Brook 1882 4, 6, 117, 140, 141,
142
- Sminthurides aquaticus* (Bourlet 1843) **138**, 140,
142
- Sminthurides pumilis*, see *Sphaeridia pumilis*
- Sminthurinus aureus* (Lubbock 1862) **166**
- Sminthurus arborealis* Itoh 1985 168
- Sminthurus marmoratus* Stach 1924 45
- Sminthurus mendenbergae* Snider 1983 91
- Sminthurus nigromaculatus* (Tullberg 1872) 45
- Sminthurus* sp. 160
- Sminthurus viridis* (Linnaeus 1758) 3, **10**, **17**, 18,
42, 45, 59, 71, 84, **88**, 105, 113, 124, 130–1,
132, 136, **137**, 139, **141**, 174, **197**, **198**
- Sphaeridia pumilis* (Krausbauer 1898) 139, **166**
- Sphaeridia* sp. **40**, 108
- Spinactaletes myoptesimus* Soto Adames 1989 **35**
- Spinactaletes* sp. 35
- Spinisotoma* sp. 90, 156
- Spinotheca* sp. 42
- Stenaphorura quadrispina* (Börner 1901) (placed in
a new genus *Stenaphorurella* by Lucianez and
Simon 1992d) **165**
- Sturmium epiphytus* Bretfeld 1994 4, 42
- Superodontella* sp. 34, **52**
- Temeritas* sp. 42
- Tetracanthella arctica* Cassagnau 1960 44
- Tetracanthella pyrenaica* Cassagnau 1953 **52**
- Tetracanthella sylvatica* Yosii 1939 **170**, **172**
- Tetradontophora bielensis* (Waga 1842) 2, 34,
59, 81, 104, 149
- Tetradontophora* sp. **92**
- Thaumanura ruffoi* Dallai 1969 81
- Tomocerura* sp. 15, 103, 160
- Tomocerus cuspidatus* Börner 1909 153, 168
- Tomocerus flavescens*, see *Pogonognathellus
flavescens*
- Tomocerus ishibashii* Yosii 1954 142–9, **143**, **144**,
145, **146**, **147**, **148**
- Tomocerus longicornis*, see *Pogonognathellus
longicornis*
- Tomocerus minor* (Lubbock 1862) 100, 101,
104–5, 114, **114**, 124, 149, **149**, 152, **166**, 200
- Tomocerus minutus* (Tullberg 1876) 149
- Tomocerus problematicus* Cassagnau 1964 114,
114
- Tomocerus* sp. 38, 90, **104**, 168
- Tomocerus varius* Folsom 1899 **170**, **172**
- Tomocerus vulgaris* (Tullberg 1871) 116
- Tritomurus falcifer* Cassagnau 1957 **182**
- Troglopedetes delamarei* Massoud and Gruia 1974
182
- Tullbergia callipygos*, see *Paratullbergia
callipygos*
- Tullbergia krausbaueri*, see *Mesaphorura
krausbaueri*
- Tullbergia quadrispina*, see *Stenaphorura
quadrispina*
- Tullbergia yosii*, see *Mesaphorura yosii*
- Typhlogastrura* sp. 76
- Uralaphorura* sp. 93
- Vertagopus arboreus* (Linnaeus 1758) 9, **11**
- Wankeliella mediochaeta* Rusek 1975 **165**
- Willemia* sp. 15
- Willemia anophthalma* Börner 1901 **52**, 156, **165**
- Willemia aspinata* Stach 1949 = junior synonym of
Willemia denisi

Willemia denisi Mills 1932 **165**

Willowsia jacobsoni (Börner 1913) 41

Xenylla boernerii Axelson 1905 108, **108**

Xenylla jocquei André 1988 70, 84, **86–7**

Xenylla sp. 30, 45

Xenylla xavieri Gama 1959 **176**

Yuukianura sp. **52**

Zebulonia massoudi Betsch 1970 138